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THE KILLER WHALE

Foraging Specializations and Group Hunting

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AMONG THE cetaceans, killer whales (*Orcinus orca*; fig. 5.1) exhibit several unusual features related to social organization, ecology, and behavior. Perhaps the most striking of these features are their dispersal patterns. For two so-called *resident* populations in the eastern North Pacific (numbering about two hundred and eighty-nine individuals, respectively, as of 1998), neither sex has been recorded dispersing (neither locational nor social dispersal—cf. Isbell and van Vuren 1996) from their natal groups over a twenty-one-year period, nor has immigration into a group been recorded (Bigg et al. 1990b). Natal philopatry by both sexes has not been positively documented for any other population of cetacean or, for that matter, for any other species of mammal. Individuals from *resident* populations feed on fish, and individuals from another, sympatric population, *transients*, specialize on marine mammal prey. These two forms were termed *resident* and *transient* based on research in the 1970s (Bigg et al. 1976; Bigg 1982). These names have been shown subsequently not to be particularly descriptive of the movement patterns and site fidelity of the two forms (Guinet 1990; Baird et al. 1992), but they have been retained as the common names. One apparent consequence of the differences in diet is the differences in dispersal patterns. *Resident* killer whales travel in long-term stable groups made up of several maternal lineages (Bigg et al. 1990b). However, among *transients*, all female offspring and all but one male offspring seem to disperse from their maternal groups (social dispersal), but dispersing offspring continue to use their natal range (locational philopatry) (Baird 1994). Besides the difference in diet, *resident* and *transient* killer whales also differ in behavior, acoustics, morphology, pigmentation patterns, and genetics (table 5.1; fig. 5.2).

Foraging specializations appear to occur in killer whale populations elsewhere, though research efforts have been generally insufficient to determine whether, as in the North Pacific populations, sympatric forms specialize on different prey types. Individuals of some Southern Ocean populations feed almost exclusively on marine mammals (Hoelzel 1991a; Guinet 1991b; Baird et al. 1992). Predation on marine mammals makes the study of foraging behavior easier than perhaps for any other species of cetacean because the prey are large, breathe at the surface, and are often captured close to, or even on, shore. Several interesting findings have come from these studies, including apparent teaching of hunting skills to offspring (Lopez and Lopez 1985; Guinet 1991a; Hoelzel 1991a) and a strong relationship between group size and foraging success in one population (Baird and Dill 1996). Other studies have demonstrated features for killer whales that appear to be unusual among mammals in general, including the presence of some females who live twenty or more years beyond the birth of their last known offspring (Olesiuk et al. 1990) and the occurrence of group-specific vocal dialects within killer whale populations (Ford and Fisher 1983; Strager 1995). In this chapter I review the general biology of killer whales, focusing on several longitudinal studies on free-ranging animals. Information on feeding habits, ranging patterns, and social organization and behavior is emphasized.

Taxonomy

The killer whale is a member of the suborder Odontoceti, family Delphinidae, subfamily Orcininae. The member-



Figure 5.1. An adult female *transient* killer whale porpoising off Victoria, British Columbia. (Photograph by Robin W. Baird.)

ship of the subfamily Orcininae has not been agreed upon, however (Heyning and Dahlheim 1988); some include only the genus *Orcinus* and the false killer whale (*Pseudorca crassidens*), others include only *Orcinus* and the Irrawaddy dolphin (*Orcaella brevirostris*), while still others include the pilot whales (*Globicephala* spp.) and pygmy killer whale (*Feresa attenuata*) in addition to *Orcinus*, *Orcaella*, and *Pseudorca*. At present, only one species in the genus *Orcinus* is generally recognized, *O. orca*. Several authors have suggested recently that there is more than one species in the genus. Based on animals killed in Soviet whaling operations in the Antarctic, Mikhalev et al. (1981) and Berzin and Vladimirov (1983) independently described new species in the genus (*O. nanus* and *O. glacialis* respectively), both of which seem to refer to the same population, with a smaller average body size than *O. orca* (Heyning and Dahlheim 1988). Berzin and Vladimirov (1983) also noted differences in morphology, group size, and diet, with the species

they described, *O. glacialis*, feeding primarily on fish and being found in large groups (150 to 200 individuals), while *O. orca* fed mainly on marine mammals and was found in smaller groups (10 to 15 individuals). While the proposed new species differed somewhat in habitat from *O. orca* (*O. glacialis* was found in among the ice floes while *O. orca* was found in open water), their ranges, based as well on the data from Mikhalev et al. (1981), did overlap. Neither of these new designations have been generally accepted (Perrin 1982; Heyning and Dahlheim 1988). Based primarily on behavioral and ecological data, Baird (1994) has argued that the two sympatric forms in the nearshore waters of the eastern North Pacific (one feeding on fish and the other feeding on marine mammals) are reproductively isolated and, thus, should be considered separate species. However, the use of a morphological species concept by cetacean taxonomists, rather than a reproductive one, makes such a suggestion unlikely to be accepted (Baird 1994).

Table 5.1. Differing characteristics of *resident* and *transient* killer whales in nearshore waters of the eastern North Pacific

Morphology/genetics

Shape of dorsal fin (Bigg et al. 1987; Bain 1989)

Saddle patch pigmentation (Baird and Stacey 1988)

Possibly eye patch pigmentation (D. Ellifrit, personal communication, cited in Baird 1994)

Mitochondrial and nuclear DNA (Stevens et al. 1989; Hoelzel and Dover 1991a; Hoelzel et al. 1998a)

Behavior/ecology

Diet (Bigg et al. 1987, 1990a; Morton 1990; Baird and Dill 1996)

Travel patterns/habitat use (Heimlich-Boran 1988; Morton 1990; Baird and Dill 1995)

Respiration patterns (Morton 1990)

Vocalizations (Ford and Hubbard-Morton 1990; Morton 1990)

Echolocation (Barrett-Lennard et al. 1996a)

Amplitude of exhalations (Baird et al. 1992; Baird 1994)

Possibly diving patterns (Baird 1994)

Group size (Bigg et al. 1987; Morton 1990; Baird and Dill 1996)

Pattern and extent of natal philopatry (Bigg et al. 1987; Baird and Dill 1996)

Seasonal occurrence (Guinet 1990; Morton 1990; Baird and Dill 1995)

Geographic range (Bigg et al. 1987)

Ecology and Social Organization

Field Studies

Prior to the 1970s, little was known of the biology of killer whales. Occasional observations of stranded animals or animals taken in whaling operations, as well as anecdotal observations of the behavior of animals in the wild and a few captive individuals, were recorded (see, for example, Carl 1946; Backus 1961; Caldwell and Brown 1964; Newman and McGeer 1966; Rice 1968). Detailed field studies on killer whales were first initiated in the early 1970s and have been undertaken in several nearshore locations around the world (Bigg et al. 1990b; Guinet 1990; Lopez and Lopez 1985; Lyrholm 1988). These studies have relied on photo-identification of individuals, based on distinctive acquired and congenital characteristics of the dorsal fin and the saddle patch, a lightly pigmented area just below and behind the dorsal fin. All killer whales in an area can be identified with high-quality photographs. Focal sampling is relatively easy with killer whales because their morphological characteristics (large size, distinctive dorsal fin and saddle patch, sexual dimorphism) allow for rapid individual identifica-

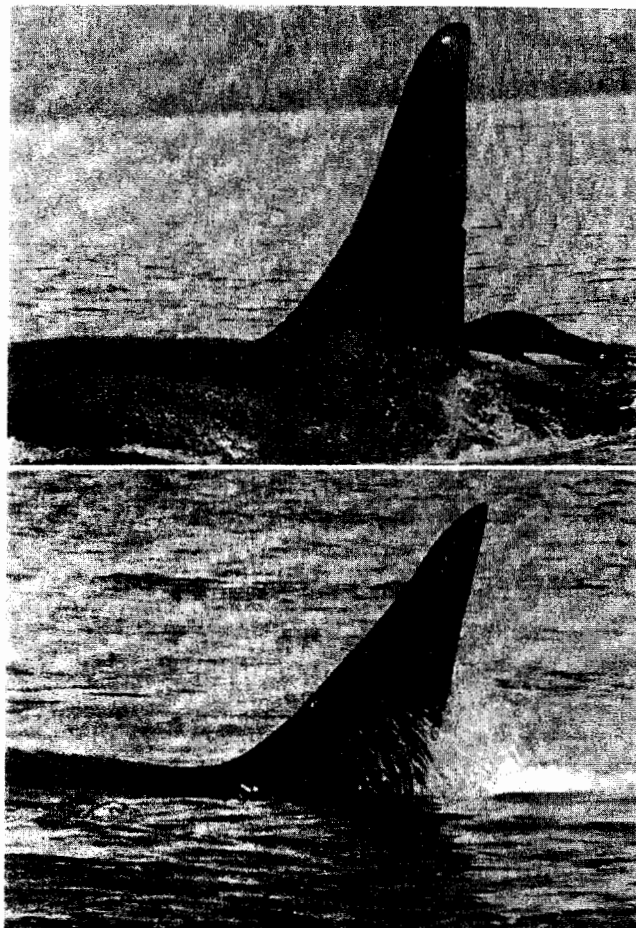


Figure 5.2. Adult male *resident* (top) and *transient* (bottom) killer whales from British Columbia, showing differences in dorsal fin shape (typically *resident* dorsal fins are more rounded).

Saddle patch pigmentation patterns also differ, with some *residents* (including the example shown here) having black pigmentation intruding into the grayish-white saddle patch, while *transients* do not (see Baird and Stacey 1988).

(Photographs by Robin W. Baird.)

tion. Photo-identification of killer whales has been utilized in many localities (e.g., Sigurjónsson et al. 1988; Black et al. 1997), but in four areas in particular, long-term studies of identified individuals have been undertaken (e.g., Bigg et al. 1990b; Hoelzel 1991a; Guinet 1991b; Bisther and Von-graven 1995; Similä et al. 1996). I discuss each of the four areas in detail below.

British Columbia, Washington, and Alaska. Spong et al. (1970) initiated the first field study of killer whales in British Columbia, but this early work did not incorporate photo-identification of individuals. Its primary goal was to examine the behaviors of wild individuals, following on Spong's earlier research on captive animals (e.g., White et al.

1971). Population studies utilizing photo-identification, initiated in response to a live-capture fishery (in which animals were taken for captivity), began both in British Columbia and in the state of Washington in 1973 and have continued to date (Balcomb et al. 1982; Bigg 1982; Bigg et al. 1990b; Olesiuk et al. 1990). The proximity of these areas to large human population centers and the ease of working in the calm inshore waters attracted numerous investigators to work there. Most of the research focused on *residents*, which were predictably found in particular locations at certain times of the year. In early years, research efforts were focused in two specific areas: Johnstone Strait, off northeastern Vancouver Island, and Haro Strait, an area that straddles the border between the United States and Canada off the southern tip of Vancouver Island. These areas were the focus of virtually all research on killer whales in British Columbia from 1973 through the late 1980s. Only in the early 1990s did research begin to encompass a broader geographic range within British Columbia, with further work in the Strait of Juan de Fuca, off the west coast of Vancouver Island, and in areas in northern British Columbia and the Queen Charlotte Islands. Studies in British Columbia and Washington have provided the most detailed information on killer whales anywhere in the world. The early photo-identification studies provided a basis for numerous behavioral and ecological studies. Some of these later studies were initiated in the late 1970s, but most were started in the 1980s, covering a diverse range of topics, including foraging and feeding (J. R. Heimlich-Boran 1986; Felleman et al. 1991; Nichol and Shackleton 1996), vocal traditions and vocal behavior (Hoelzel and Osborne 1986; Ford 1989, 1990), habitat use (Heimlich-Boran 1988; Hoelzel 1993), life history and population dynamics (Olesiuk et al. 1990; Brault and Caswell 1993), and social behavior and social structure (Haenel 1986; S. L. Heimlich-Boran 1986; Bigg et al. 1990b; Rose 1992).

Residents in British Columbia appear to be divided into two geographic populations, one termed the "northern" *residents*, usually found off northern Vancouver Island and in southeastern Alaska (Dahlheim et al. 1997), and the other termed the "southern" *residents*, usually found off southern Vancouver Island and in Washington. Considerably less research has been undertaken on the *transient* population. Commercial production of a catalog of known individuals, both *residents* and *transients*, in 1987 (Bigg et al. 1987), greatly facilitated matching of individuals between areas and comparisons between studies. An updated version containing only individuals from the *resident* population was produced in 1994 (Ford et al. 1994), and a catalog of all individuals found in southeastern Alaskan waters, in-

cluding both *resident* and *transient* individuals found farther south in British Columbia, was produced in 1997 (Dahlheim et al. 1997). Comparisons between areas for *transients* documented since the 1987 catalog are undertaken primarily through the exchange of photographs by researchers working at various institutions (e.g., Baird 1994; Dahlheim et al. 1997).

Largely in response to the potential for live-capture fisheries in Alaska, research on killer whale population size and dynamics was begun in Prince William Sound in 1983 and in southeastern Alaska in 1984 (Leatherwood et al. 1984, 1990) and has continued to date (Matkin and Saulitis 1994; Matkin et al. 1994; Dahlheim et al. 1997). Production of catalogs of known individuals from these areas (Heise et al. 1991; Dahlheim et al. 1997) has facilitated studies within each area as well as comparisons between them.

Argentina (Patagonia). Lopez and Lopez (1985) initiated behavioral research on killer whales in the nearshore areas of Punta Norte, Peninsula Valdés, southern Argentina, in 1975. Southern elephant seals (*Mirounga leonina*) and southern sea lions (*Otaria byronia*) utilize beaches in that area and give birth to their pups in September and October and from January to February respectively. These are also the time periods when killer whales are most commonly seen swimming close to the coast, preying mainly on pups and juveniles, but sometimes on adults. In this area, intentional stranding on shore to capture hauled-out prey is the primary foraging tactic (Lopez and Lopez 1985; Hoelzel 1991a). Research efforts at this site have been largely land-based examinations of the behavior of individuals foraging in nearshore areas.

Norway. Photo-identification studies in Norway were initiated in 1983, largely in response to management needs for population estimates in the area, where extensive hunting of killer whales had been conducted for over forty years (Lyrholm 1988). Boat-based photo-identification studies have been conducted both around the Lofoten and Vesterålen islands, in northern Norway, and around the More area in southwestern Norway (Lyrholm 1988). Killer whales are most abundant in those areas between October and January, when they follow the movements of herring (*Clupea harengus*) into nearshore areas (Bisther and Vøngraven 1995; Similä et al. 1996). Studies on acoustic and feeding behavior have also been possible in the protected waters of enclosed fjords (Similä and Ugarte 1993; Strager 1995; Similä et al. 1996).

Crozet Archipelago. Killer whales are the most frequently seen cetacean in the nearshore waters of Possession Island, Crozet Archipelago, located in the southwestern Indian

Ocean. They can be found in that region year-round and can be seen daily from October to December at Possession Island, where they feed on a wide variety of prey, including elephant seals, penguins, fish, and other whales (Guinet 1991b). Guinet studied this population from 1987 through 1990, primarily to examine behavior and ecology and to make comparisons with other killer whale populations (Guinet 1991b, 1992). Research in the area has been largely land-based. Marine mammals are the most frequent prey observed taken, and intentional stranding to capture prey hauled out on shore is regularly recorded.

Comparisons between sites and data collection. As noted, methods at these different field sites have varied. Such differences are due both to site-specific conditions and to differing numbers of researchers working at each site. Research in the Crozet Archipelago and in Patagonia has been primarily shore-based and undertaken by a very small number of investigators. Studies in all areas have been largely restricted to small geographic areas for only a few months of the year, when weather conditions are best (British Columbia and Washington) or when killer whales move into nearshore areas (Norway). Seasonal differences in the occurrence of pods that use extremely nearshore areas (within a few hundred meters of shore), combined with pod-specific and seasonal differences in behavior (Baird and Dill 1995), all bias data collected at different sites as well as comparisons between sites.

Encounters with killer whales at shore-based sites are typically limited in duration because of the small geographic area covered. Killer whales are detected visually (Punta Norte) and/or acoustically (Crozet Archipelago) with hydrophones as they move toward these land-based sites. Primarily boat-based research sites, such as British Columbia, Washington, Alaska, and Norway (although there are several land-based studies in British Columbia and Washington running concurrently with boat-based studies), have typically covered wider geographic areas. Detection of killer whales utilizing these areas has relied on a combination of land-based observers, radio reports from commercial fishermen or whale-watching charter operators, hydrophones deployed from shore, and boat-based surveys looking for killer whales. Virtually no research has been undertaken at night in any of these areas, due to the difficulty in tracking and observing killer whales at night. For larger groups (more than ten individuals), boat-based tracking can be undertaken for extended periods of up to ten or twelve hours. For smaller groups (fewer than four individuals), extended tracking can be more difficult. This is especially true for *transient* killer whales, which travel

in smaller groups, dive for longer periods, and follow less predictable routes (Morton 1990; Baird and Dill 1995). For both photo-identification and behavioral studies, killer whales are typically tracked from distances ranging from 10 to several hundred meters. For behavioral studies, most researchers have relied on following particular groups or, less frequently, focal animal sampling.

Distribution and Seasonal Occurrence

Killer whales are cosmopolitan, having been observed in all oceans of the world. However, concentrations generally occur in colder regions and in areas of high productivity (Bigg et al. 1987; Heyning and Dahlheim 1988; Guinet and Jouventin 1990). No clear evidence of seasonal north-south migrations is available. Based on sightings from whaling vessels in the Southern Hemisphere, Mikhalev et al. (1981) described seasonal migrations from high-latitude areas (most south of 50°S) in the summer months to lower-latitude areas (most north of 50°S) in winter. However, no information was presented on potential seasonal biases in effort, and the conclusions were based on densities of whales recorded in particular areas, not on movements of individual animals, so it is difficult to judge the validity of such conclusions (Perrin 1982). In polar areas, the occurrence of killer whales may be limited by the presence of pack ice in the winter months, thus some north-south movements would have to occur (Reeves and Mitchell 1988a). However, a recent sighting of killer whales deep in Antarctic sea ice in winter indicates that not all individuals move away from the poles (Gill and Thiele 1997). The extreme seasonal biases in effort could be partly responsible for the perception that all killer whales move toward lower latitudes in the winter months (Gill and Thiele 1997). Killer whales are present year-round in many areas. Evidence suggests that individuals occupy very large ranges (see, e.g., matches between California, Oregon, British Columbia, and Alaska presented in Black et al. 1997), and the proportion of time spent in different parts of their ranges may vary seasonally.

In the British Columbia and Washington study areas, both *resident* and *transient* killer whales are present year-round. Several authors have suggested that *residents* are rare in the core study areas during the winter months due to the decreased presence of salmon (*Oncorhynchus* spp.), one of their primary prey species (J. R. Heimlich-Boran 1986; Bigg et al. 1987; Nichol and Shackleton 1996). Several seasonal biases in effort are present, however. In general, less effort has been extended in the winter months. Inclement weather conditions and low daylight hours during the

winter months also likely decrease the probability of visually detecting killer whales when they are present. Seasonal comparisons of vocalization rates among *resident* killer whales in Johnstone Strait suggest decreased presence during the winter months (Nichol and Shackleton 1996). However, possible biases include a decreased rate of vocalizations by *residents* during the winter months (D. E. Bain, personal communication) and use of travel routes farther from shore during these times (R. W. Baird, personal observation), thus affecting visual or acoustic detection from shore. Methods for measuring salmon abundance have also been indirect, relying on sports fishing catches, commercial catches, and the number of salmon arriving at spawning rivers (J. R. Heimlich-Boran 1986; Nichol and Shackleton 1996). Until these issues are resolved, correlations between the seasonal presence and abundance of killer whales and prey availability remain unclear. During periods when effort is relatively high, however, there is a general correlation between the presence and/or number of killer whales using an area and the relative abundance of salmon (J. R. Heimlich-Boran 1986; Nichol and Shackleton 1996). Such a correlation implies that availability of prey may limit the number of killer whales that use an area. Different northern *resident* pods may correlate with different runs and/or different species of salmon (Nichol and Shackleton 1996), suggesting that pods have different primary foraging areas within their overlapping home ranges and that temporal segregation may occur for some pods that share primary foraging areas.

Seasonal influxes into nearshore areas where pinnipeds are abundant have been noted for killer whales around Marion Island, the Crozet Archipelago, and Punta Norte, Argentina (Condy et al. 1978; Guinet 1992; Hoelzel 1991a). For *transient* killer whales in southern British Columbia, a strong seasonal peak occurs, coinciding with the period when harbor seal (*Phoca vitulina*) pups are being weaned (Baird and Dill 1995). This peak was not due to a general increase in the visitation by *transients* of this area; rather, some pods of *transients* appeared to use this area preferentially during pup weaning while others were seen there regularly year-round. Those pods that used the area year-round also tended to travel farther from shore (typically more than 1 km). The general result was that pods present during fall through spring typically spent more time away from the shoreline; therefore, land-based observers or spotters were less likely to notice them. Due to this seasonal difference in use of nearshore areas, many shore-based studies may be biased when examining seasonal presence (Baird and Dill 1995). Even boat-based studies typically have focused on nearshore areas (within 20 km of

shore); because of this bias, it is unknown where individuals go when not in nearshore areas.

Social Organization

Killer whale groups vary in size from single animals to as many as several hundred individuals (Perrin 1982). However, larger groups appear to be temporary associations of smaller, more stable groups. In all areas where longitudinal studies have been carried out, evidence suggests that there are long-term associations between individuals and limited dispersal from maternal groups (Lopez and Lopez 1985; Bigg et al. 1990b; Guinet 1991b; Similä and Ugarte 1993; Baird 1994; Baird and Dill 1996). Such evidence is most conclusive for the British Columbia and Washington study areas, and this area also has the best data for variability in group size, structure, and stability, showing differences in these characteristics between the sympatric *residents* and *transients*.

Groups of killer whales have been defined and categorized based on spatial associations, synchronization of respirations, acoustic dialects, and coordination of activity. Categorizations of groups and associations have varied between studies. Associations within groups have generally been based on distance between individuals during observations (Rose 1992) or on presence together in the same photographic frames during photo-identification studies (S. L. Heimlich-Boran 1986; Bigg et al. 1990b). Groups have been defined by general presence in an area (S. L. Heimlich-Boran 1986; Bigg et al. 1990b) or as all individuals swimming within 100 m of each other (Lopez and Lopez 1985). Baird (1994) defined group membership for *transients* as when all whales, within visual range of observers, acted in a coordinated manner during an observation period. This definition could include individuals up to a kilometer or more apart, when coordination of activities was made apparent by individuals converging on a single prey item discovered by one member of the group. Such a definition of group membership typically required an extended period of observation; determination of group membership was often not possible for short-duration encounters (for example, those of less than fifteen minutes).

Resident pods, subpods, and matrilineal groups. Over a fifteen-year period, Bigg et al. (1990b) studied the social organization of two populations of *resident* whales (totaling about 260 individuals at the end of the period). Multiple encounters each year with all three pods in one population and most of the pods in the other population allowed for detailed examination of *resident* social organization. Information was collected year-round, though there was a sea-

sonal bias, with most data collected between June and September. *Resident* social organization was classified as a series of progressively larger groups, with each category showing no changes in membership, either seasonal or long-term (Bigg et al. 1990b). The smallest group is termed a matrilineal group or intrapod group. The researchers found that an individual only very rarely separated from its intrapod group for more than a few hours. These groups are of mixed age and sex and range in size from two to nine individuals (mean = 4). They appear to contain a single matriline of from one to four (mean = 3) generations, with both male and female offspring found in association with the oldest female in the group. Subpods comprise one to eleven (mean = 2) matrilineal groups and are defined as matrilineal groups that spend more than 95% of their time traveling together. These matrilineal groups are thought to be more closely related to each other than to other matrilines within the pod (Bigg et al. 1990b). Pods comprise from one to three (mean = 2) subpods and are defined as groups of subpods that travel together more than 50% of the time; pod memberships were determined with repeated observations over a period of years. Average pod size in the two populations combined was approximately twelve individuals (range of three to fifty-nine individuals).

Resident dispersal. Evidence for lack of dispersal from natal groups by *residents* is conclusive, based on the long-term stable associations observed, the lack of resightings of any individuals outside of their natal range or away from their natal pod, even with considerable research effort over a twenty-one-year period, and adult survival rates. One hundred and thirty-four individuals were born into the two populations during the duration of the study. Fifty-nine individuals disappeared, and none of those individuals were ever sighted again in the company of other whales (all were thought to have died). Additionally, none of the individuals that have disappeared have been sighted in groups of *resident* killer whales observed in the adjacent waters of southeastern Alaska. Individuals that disappeared ranged in age from newborn calves to old adults, with both sexes represented. Disappearance rates (= presumed mortality rates) did vary with age and sex (Olesiuk et al. 1990), but the individuals that disappeared at the highest rates (calves younger than five years, males older than twenty-five years, females older than fifty years) were those least likely to have dispersed, according to current thought regarding mammalian dispersal patterns. Additionally, if more than a couple of the older individuals that disappeared had actually dispersed and survived, the already high survival rates of adults (see below) would be unrealistically inflated. Concurrent

studies by other investigators on the same populations, an additional six years of data collected subsequent to the study reported by Bigg and his colleagues (Ford et al. 1994), and research on *resident* populations in Alaska (Matkin et al. 1994) also support the lack of dispersal noted.

Cohesion and splitting of resident pods. As noted, *resident* pods are defined as groups of subpods that spend more than 50% of their time together over a period of years. Such a definition does not do justice to the wide range of circumstances in which pods can be encountered. Members of one or more subpods can be encountered in extremely close proximity to one another (as many as fifty-nine individuals clustered within less than 100 m of each other) or spread out over several kilometers. On some occasions, subpods may join and leave each other over the space of hours or days, while during other periods, the entire pod can be seen together repeatedly for days on end, with all individuals present. Some evidence also exists of seasonal trends in pod spacing: during the winter months individuals within a pod often appear to be spread out over much larger areas (D. E. Bain, personal communication; R. W. Baird, personal observation). Such variability means that definitions of "pods" in other study areas may require numerous repeated observations of groups, both within and between years. *Resident* pods are thought to form due to the splitting of a single pod into two or more over a period of many years, perhaps decades (Ford 1990; Ford et al. 1994). Based on the "50% rule," two pods of *residents* (one northern and one southern) appear to have split since the British Columbia study began in 1973. No quantitative analysis is available in either case, but in both cases, three subpods were seen together for the majority of sightings in the 1970s, but gradually spent less and less time together during the 1980s, and in the 1990s are usually not seen together (Ford et al. 1994; R. W. Baird, personal observation; D. K. Ellifrit, personal communication). Ford et al. (1994) speculated that the death of the oldest female in the group, from whom many of the individuals are usually descended, can destabilize a pod or subpod and begin the process of pod splitting.

Acoustic clans as a measure of resident grouping. Ford's research on *resident* killer whale acoustics demonstrated the existence of stable pod-specific dialects and showed that some pods shared a number of calls (Ford 1990; Ford and Fisher 1983). He suggested that shared calls between pods reflect common ancestry. Taking into account both association patterns and pod-specific vocal repertoires, within British Columbia and Washington, *resident* social organiza-

tion can be further categorized for groups greater than the level of pods. Acoustic clans can be defined as pods that share one or more calls (Ford 1990). Four acoustic clans have been identified for British Columbia and Washington *residents*. Three of these clans share a common range and regularly associate with each other off northern Vancouver Island, northern British Columbia, and southeastern Alaska (the "northern" *residents*). A fourth clan, whose members have not been observed associating with individuals in the three northern clans (the "southern" *residents*), is usually found off southern Vancouver Island and in Washington. The southern *resident* community contained eighty-nine individuals as of 1998. The northern *resident* community has been reported to contain about two hundred individuals (Ford et al. 1994), but some pods within this community have been seen interacting with *resident* killer whales in southeastern Alaska (Dahlheim et al. 1997), which in turn have been observed interacting with *residents* in Prince William Sound, Alaska (Matkin et al. 1997); thus the population size of northern *residents* is likely much greater.

Resident interpod and intrapod associations. Pods within a community are frequently observed associating with one another, particularly during the summer months. The presence of high prey concentrations during these months could simply result in an aggregation of whales in an area of high food availability, or, conversely, it could allow whales to congregate for social purposes without the cost of increased competition for prey. One unusual behavior observed among southern *resident* killer whales when meeting during these periods has been termed a "greeting ceremony" (Osborne 1986). A greeting ceremony occasionally occurs when two or more pods meet after having been separated for more than a day. When this happens, individuals within each pod have been observed in a line abreast formation at the surface, facing the other pod. They approach each other, and at a distance of 10–20 m, they remain motionless for approximately ten to thirty seconds. Both pods have then been observed to submerge and swim toward the other, so that when they resurface, they form tight mixed groups, a common feature of intermingling behavior (Osborne 1986). Social and sexual behavior is frequently observed during greeting ceremonies and in associations of up to a hundred individuals. The increased social and sexual behavior in large associations suggests that pods come together for social interactions when competition for prey is reduced. There is no clear evidence of territoriality between pods within either the northern or southern *resident* communities. If killer whales are not territorial, it would

no doubt relate to their large home ranges (cf. Mitani and Rodman 1979).

Since no dispersal of either sex occurs from *resident* pods, breeding is likely to occur between pods rather than within a pod (although cf. Hoelzel et al. 1998a). The presence of reproductively active females within pods containing no adult males (e.g., Bigg et al. 1987) also suggests that breeding must occur between pods. The increased frequency of sexual behavior in multipod associations also supports this supposition. Copulation between an adult male and an adult female has rarely been positively documented in the wild, however, and genetic data are not yet available to positively confirm that mating occurs between *resident* pods.

It has been erroneously reported in the literature that the northern and southern *resident* communities have non-overlapping ranges (for example, Bigg et al. 1990b; Felleman et al. 1991). In fact, their ranges overlap by over 120 km on both the east and west coasts of Vancouver Island. Behavioral interactions have not been observed between individuals from the different *resident* communities, although relatively little research has been undertaken in the areas where the populations overlap. Core areas have been identified for each community, and these are separated by about 390 km (2.5 days of travel at 3.5 knots: Bigg 1982). Differences in pigmentation patterns suggest that the communities may be reproductively isolated (Baird and Stacey 1988). Genetic analyses have been undertaken using samples collected from stranded, captive, and free-ranging animals (Stevens et al. 1989; Hoelzel and Dover 1991a; Hoelzel et al. 1998a). Mitochondrial DNA comparisons within the northern and southern *resident* killer whale populations have demonstrated no variability (Hoelzel et al. 1998a). A comparison between the two populations found a small (one base pair) but fixed haplotype difference (Hoelzel et al. 1998a), suggesting that these populations may have arisen due to separate founding events.

Transient social organization. Less investigation into the social organization of *transient* killer whales has been undertaken. New adult and/or subadult *transient* individuals are regularly documented in the British Columbia/Washington study area (Baird and Dill 1995). In 1986 only 79 individuals had been identified in the population, while by 1993 a total of 170 individuals had been documented (Bigg et al. 1987; Ford et al. 1994). Some individuals are seen numerous times each year, but the long resighting intervals for others (up to ten years) have made positive recording of dispersal (and, for that matter, of deaths) much more difficult than for *residents*. Using Bigg

et al.'s (1990b) 50% association rule to define pods (that is, individuals that travel together more than 50% of the time over a period of years), *transients* clearly associate in distinct pods (Baird and Whitehead 1999). Each pod appears to be equivalent to a single *resident* matrilineal group, with from one to two generations present (Baird 1994; Baird and Dill 1996). Average pod size in Baird and Dill's (1996) study was two individuals, with a range from one to four individuals.

Transient dispersal. Unlike *resident* pods, definite social dispersal (Isbell and van Vuren 1996) from *transient* pods has been recorded, although only on two occasions (one of each sex: Bigg et al. 1987; Baird and Dill 1996). The two dispersing individuals were resighted within their natal range but did not associate with their natal group (locational philopatry). Extensive indirect evidence of dispersal also exists: maximum pod size appears to be four individuals, while pods containing only a single individual made up 31% of the pods recorded by Baird and Dill (1996), and *transient* pods usually contain only one adult male and/or one reproductive female. By contrast, the smallest *resident* pod recorded is three individuals, and *resident* pods often contain more than one adult male and/or more than one reproductive female. For *transients*, based on the 50% association rule, it appears that either a male or a female could be considered a pod of size one. However, this is not to say that these individuals are always found alone. All lone individual *transients* documented have been adult or subadult males (Baird 1994). Female *transients* with no offspring that appear to have dispersed from their natal group seem to travel with a variety of other *transient* pods for temporary periods. Male *transients* that appear to have dispersed spend some time alone and some time traveling temporarily with other *transient* pods (in Baird's 1994 study, of five different "lone male" pods, five of the twelve sightings of these individuals involved other pods present, while the remaining seven sightings involved only the single individual).

Transient pods are fairly stable, with some close associations (that is, they are virtually always seen together) between individual *transients* documented over fifteen years or more. Based on both direct and indirect evidence, it appears that female *transients* disperse from their matrilineal group either when they reach sexual maturity or when they give birth to their first calf, effectively forming their own pod (Baird 1994). Females without dependent offspring, as noted, and females with a young calf do not appear to travel alone. Instead, they temporarily associate with a variety of other *transient* pods. Dispersal of male *transients* occurs, but not all males seem to disperse. In one

of the two cases of dispersal recorded, a subadult male left his natal group, which also contained an adult male thought to be his maternal sibling. Based on this observation and the occurrence of, at most, one adult male in a *transient* pod, Baird (1994) suggested that all males other than the first-born disperse before the onset of sexual maturity.

Transient interpod associations. All *transient* pods documented in British Columbia that are larger than one individual in size contain an adult female, unlike those off Punta Norte, where a stable group made up of a pair of males has been observed in a study that identified thirty individuals (Lopez and Lopez 1985; Hoelzel 1991a). *Transient* pods often associate with one another; group size of *transients* noted by Baird and Dill (1996) ranged up to fifteen individuals, with a mean group size of about four individuals. No evidence of *transient* communities, as noted for *residents*, has been found, although not all *transient* pods are equally likely to occur in any particular area (Baird and Dill 1995; cf. Nichol and Shackleton 1996). Associations between *transient* pods do not appear to be completely random, however; they depend in part on pod size and the age and sex of all pod members (see below) and in part on the predominant foraging tactics exhibited by the pod. Baird and Dill (1995) demonstrated pod-specific foraging specializations in *transients*, which exhibited two general types of foraging, nearshore and offshore. Pods tended to associate more frequently with others that shared similar foraging tactics than with those that differed in terms of foraging specialization. Such associations may be due in part simply to foraging in similar habitats, but Baird et al. (1992) and Baird and Dill (1995) suggested a possible functional explanation for this pattern: individuals should associate more with others that share their foraging abilities when it is advantageous to forage cooperatively in very small groups.

Interactions between residents and transients. Bigg (1982) defined the *transient* population as a third community, in addition to the northern and southern *residents*. Early ideas regarding *transients* were that they were individuals rejected from *resident* pods (M. A. Bigg, personal communication; cited in Baird 1994) and that they had been relegated to a less desirable lifestyle with low productivity (Bigg 1979). *Residents* and *transients* have subsequently been described as "races" by several investigators (Bigg et al. 1987; Ford et al. 1994), though "race" is usually defined in a geographic sense, implying geographically isolated populations, which are typically given subspecific designation

(Mayr and Ashlock 1991). While the two forms are sympatric, behavioral evidence suggests that they remain socially isolated. Observations of *residents* and *transients* near each other have been reported on only twenty-one occasions (Jacobsen 1990; Morton 1990; Baird and Dill 1995; Barrett-Lennard et al. 1996a). Whether the two groups are on an intersecting or nonintersecting course seems to be an important determinant of reactions, although this has not always been reported. On eight occasions no change in direction of travel was recorded for either form as they passed by each other on a nonintersecting course within a couple of kilometers (Jacobsen 1990; Baird and Dill 1995). On eight occasions when on intersecting courses, *transients* have been seen changing their direction of travel, effectively avoiding the *residents* (Morton 1990; Baird and Dill 1995), while *residents* have been recorded changing their direction of travel in the proximity of *transients* three times (Morton 1990; Barrett-Lennard et al. 1996a). Relative group sizes have not been presented for all of these observations, but *residents* are typically observed in much larger groups than *transients* (Bigg et al. 1987; Morton 1990; Baird 1994). Since *residents* vocalize more frequently than *transients* (Ford and Hubbard-Morton 1990), it is likely that *transients* detect the presence of *residents* much sooner and much more frequently than the other way around (Baird and Dill 1995). Thus the cases of *residents* showing no reaction when near *transients* may be due simply to their being unaware that *transients* were nearby. *Transients* have been recorded avoiding *residents* more frequently than vice versa. One observation of aggression between the two forms (Baird and Dill 1995) involved a large group of *residents* (approximately thirteen individuals) chasing and apparently attacking a small group of *transients* (three individuals). This observation suggests a functional reason for *transient* avoidance of *residents*—the typically larger groups of *residents* may be a threat to *transients* (Baird and Dill 1995). Why *residents* would attack *transients* remains unclear; with their tendency to feed on other marine mammals, one possibility is that under some circumstances (e.g., at times of the year or in areas where other marine mammal prey are unavailable and where *transient* group size is larger than *resident* group size), *transient* groups might prey upon lone, injured, or young *residents*.

We still know little about killer whale social organization at other sites. Lone animals have also been observed off Punta Norte, and groups of as many as twelve animals have been documented (Lopez and Lopez 1985). Stable groups off Norway range from six to thirty individuals, with a median group size of fifteen individuals (Bisther and Vongraven 1995; Similä et al. 1996), while group size off

the Crozet Archipelago ranges from two to seven individuals (Guinet 1991b). In general, group size for populations that feed on fish tends to be larger than for populations that feed on marine mammals (cf. Jefferson et al. 1991). Evidence from other sites suggests long-term associations between individuals (Guinet 1991b; Hoelzel 1991a; Bisther and Vongraven 1995; Similä et al. 1996).

Habitat Use and Ranges of Pods

Several authors have discussed habitat use by *residents* and/or *transients* (Heimlich-Boran 1988; Felleman et al. 1991; Morton 1990; Hoelzel 1993; Baird and Dill 1995). Both *residents* and *transients* frequent a wide range of water depths. Both use deep areas (>300 m), but *residents* tend to spend more time in deeper water than *transients*. *Residents* occasionally move into water less than 5 m deep, but some *transient* pods spend considerable time in even shallower depths, often foraging in intertidal areas at high tides (fig. 5.3). To quantify relative distribution patterns and habitat use in the Haro Strait region, Heimlich-Boran (1988) divided the area into 4.6×4.6 km quadrats. While over twenty times the observational hours were collected for *residents* than for *transients*, he noted that for 34% of the quadrats that *transients* were recorded in, *residents* had not been documented. Baird and Dill (1995) found considerable variability in habitat use between *transient* pods, with some spending significantly more time foraging in very nearshore areas than others. Heimlich-Boran (1988) noted an increase in *resident* foraging behavior in areas of high-relief subsurface topography, along the major routes for salmon migration. Using a different measure of foraging behavior, Hoelzel (1993) found no such correlation between feeding and bottom topography for *resident* killer whales in the same area. The time frames for these two studies did not overlap, however, so it is unclear whether the different conclusions reflect the different methods or a change in whale behavior between the two time periods.

Travel routes of *transients* and *residents* differ, with *residents* more typically traveling in straight lines while *transients* often follow the contours of the shoreline and frequently enter small bays (Morton 1990; Felleman et al. 1991). More extensive data on *transients* indicate that this may be true for *transient* pods that specialize in foraging in nearshore areas (cf. Baird and Dill 1995), but not for pods that usually forage in open water.

Individual killer whales have been documented to move over very large areas. Perhaps the widest movement documented is that of a number of individuals seen both in central California and in southeastern Alaska, a linear distance of 2,660 km (Goley and Straley 1994; Black et al.



Figure 5.3. A *transient* killer whale foraging in shallow water at Race Rocks, a sea lion and harbor seal haul-out site off southern Vancouver Island, British Columbia. (Photograph by Robin W. Baird.)

1997). Actual home range sizes are unknown, primarily because virtually no photo-identification work has been done in offshore areas. For killer whales in British Columbia and Washington, utilizing the northernmost and southernmost sightings of particular pods, combined with the limited knowledge of east-west (onshore-offshore) movements, the largest documented range for a *transient* pod is 140,000 km², while the largest documented range for a *resident* pod is approximately 90,000 km². Both *resident* and *transient* individuals have been documented to move up to 160 km in one twenty-four-hour period, but groups of both types also spend extended periods in very small areas. *Resident* pods around southern Vancouver Island may be repeatedly seen off Victoria or San Juan Island for days or even weeks in a row during the summer months. At this time of the year salmon are extremely abundant, and individuals may not have to move far to find concentrations of food. *Transients* may spend several hours milling in one small area (usually a harbor seal haul-out site) and

may repeatedly visit a larger area several times in the space of a week. Saulitis (1993) studied a group of *transient* individuals in Prince William Sound, Alaska, and compared their behavior with published studies of *transients* in British Columbia. She found that the Prince William Sound individuals spent more time traveling than *transients* in British Columbia, and suggested that this may be due to a lower abundance of marine mammal prey in her area, which could force the animals to make wider-ranging movements (there were, however, differences in behavioral definitions used in the different areas, potentially confounding such comparisons).

While killer whales are regularly observed in offshore areas off British Columbia, evidence suggests that offshore populations are distinct from both the inshore *residents* and *transients*. Recent research has documented the occurrence of several large groups that have been termed "offshore" killer whales (Ford et al. 1994; Walters et al. 1992). These offshore whales appear to differ from both *residents* and

transients in several ways. Group sizes of offshore whales (ranging from two to seventy-five, but usually thirty to sixty individuals: Ford et al. 1992, 1994; Walters et al. 1992) appear most similar to those of *residents*. Range sizes of offshore whales seem to be larger than those of *residents* (see e.g., Black et al. 1997), though precise limits are unknown at this time, and offshore whales seem to differ acoustically from both *transients* and *residents* (Ford et al. 1994). Offshore whales appear to share morphological characteristics with both *residents* and *transients*, with their dorsal fins being more similar to those of *residents* and their saddle patches more similar to those of *transients* (cf. Bigg et al. 1987; Baird and Stacey 1988). While few measurements are yet available, offshore whales appear to be smaller in body size than either *residents* or *transients* (Walters et al. 1992; Ford et al. 1994). Mitochondrial DNA comparisons of these offshore animals with *residents* and *transients* suggest that they are closely related to southern *residents*, sharing the same mtDNA haplotype (Hoelzel et al. 1998a).

Diet and Foraging Behavior

Information on feeding in killer whales has come from a variety of sources. Stomach contents from animals taken in whaling operations or from stranded individuals have provided extensive information on species consumed, particularly for fish and squid. In many cases, stomach content data are the only information documenting the occurrence of different species in the diet. In recent years extensive studies have also been undertaken on killer whale feeding behavior, and anecdotal information continues to accumulate on the range of killer whale prey (e.g., Dahlheim and Towell 1994; Florez-Gonzales et al. 1994; Constantine et al. 1998). Killer whales are top predators, with an extreme range in food items reported taken, including squid, octopus, bony and cartilaginous fish, sea turtles, seabirds, sea and river otters, dugongs, pinnipeds, and cetaceans, as well as occasional reports of terrestrial mammals such as deer, moose, and pigs (Heyning and Dahlheim 1988; Guinet 1992; Jefferson et al. 1991). Extensive stomach content data (Nishiwaki and Handa 1958; Rice 1968), numerous scattered published reports (reviewed by Hoyt 1990), and observations of behavioral interactions with other marine mammals, both predatory and nonpredatory (reviewed by Jefferson et al. 1991), provide a wealth of data on prey types. Individual populations of killer whales appear to specialize in particular types of prey (Felleman et al. 1991; Jefferson et al. 1991; Baird et al. 1992). Although most prey are taken in the water, killer whales regularly beach themselves to take prey in the Crozet Archipelago and at Punta Norte, Argentina.

Resident killer whales in British Columbia, Washington, and Alaska appear to feed primarily on fish (Bigg et al. 1990a; Matkin and Saulitis 1994). In an observation study, 95% of the fish kills observed were salmonids, and of these, 50% were one species, chinook (*Oncorhynchus tshawytscha*), the largest species occurring in that area (Bigg et al. 1990a). It seems likely, however, that salmon, particularly chinook, are disproportionately recorded by such observational methods. One reason is that salmon are typically found in the upper portions of the water column (see discussion and references below) and thus are more likely to be seen than deeper-water fish during prey chases or if prey handling is of short duration. Chinook, being the largest species of salmon, may take longer to consume and may be more likely to be shared between individuals as well. Observations of predation on bottom fish have been rare in the behavioral studies undertaken, probably because killer whales are unlikely to bring prey caught at the bottom to the surface, but stomach contents from the occasional stranded animal suggest that predation on bottom fish occurs regularly (Baird 1994; Ford et al. 1994). During their migration toward breeding rivers, salmon tend to be found primarily in schools, while juvenile salmon and overwintering adults tend to be more solitary. *Residents* have occasionally been observed feeding on herring (Ford 1989), a schooling species, but the species of bottom fish recorded are typically solitary.

Diving behavior. Little has been published on the diving behavior or diving capabilities of killer whales. An early report of an animal entangled in a submarine cable brought up from 1,030 m in depth (Heezen and Johnson 1969) suggested that killer whales can dive deeply; however, it is unclear whether this animal was entangled in the cable while diving to that depth or if it had become entangled after death or while the cable was being brought to the surface. The U.S. Navy used two killer whales in their deep object recovery program and trained one of the animals to dive to a depth of 260 m (Bowers and Henderson 1972). The use of killer whales in that project was discontinued suddenly (one animal became sick and the other escaped), so the depths recorded were not considered to be the maximum depth attainable. Baird (1994; Baird et al. 1998) used recoverable time-depth recorders (TDRs) on free-ranging killer whales and collected data from twenty-one individuals (twenty *residents* and one *transient*), for periods ranging from fifteen minutes to over thirty hours. Whales were usually tracked visually while tagged; thus information on behavior was collected simultaneously with diving data. Diving patterns of *residents* were extremely variable while

foraging. Some long-duration dives were very shallow (e.g., less than 10 m), some were to midwater, and some were to the bottom, in depths up to 260 m (fig. 5.4). While regularly diving deeply, the *residents* spent the vast majority of their time (more than 70%) in the top 20 m of the water column. The limited information available on the depth distribution of salmon in that area suggests that most species spend the vast majority of their time in the upper levels of the water column (that is, less than 30 m: Quinn and terHart 1987; Quinn et al. 1989; Ruggerone et al. 1990; Olson and Quinn 1993; Baird 1994), so the time spent by *residents* in the upper levels of the water column may reflect their regular predation on salmon. Foraging *residents* did dive regularly to the bottom, however (Baird 1994; Baird et al. 1998), and such behavior may reflect predation on bottom fish, as has been noted from stomach contents.

Diving behavior has been recorded for only a single *transient* (Baird 1994). Some obvious differences from *resident* diving behavior were apparent, but clearly more data are necessary to confirm whether such differences consistently occur between the two forms. It is worth discussing the diving behavior of the *transient*, though, as it may be relevant to prey detection. The diving pattern of the *transient* was extremely regular, with all long-duration dives (between one and seven minutes) being to depths between 20 and 60 m. The individual spent more than two-thirds

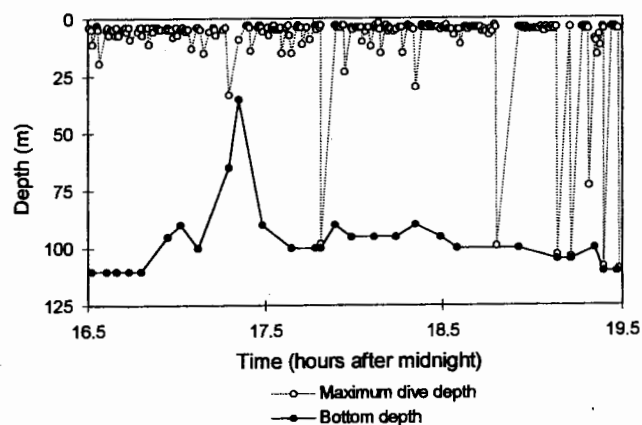


Figure 5.4. An example of the diving pattern of a *resident* killer whale. This animal (a thirteen-year-old male) was followed while tagged for the three hours shown here and was considered to be foraging. The bottom depth was recorded periodically during this period (shown by solid line). The distance traveled over this period was approximately 20 km, thus the steepness of bottom contours is exaggerated. Only a single point is shown for each dive, representing the maximum depth. On some occasions the animal dove to the bottom in up to 100 m of water, similar to all foraging *residents* in the study by Baird (1994; Baird et al. 1998). (From Baird 1994.)

of its time between 20 m and 60 m in depth. The behavior of the animal was classified as foraging during this time, so it appears unlikely that the observed pattern differed from that of the *residents* due to a difference in behavioral state. Baird (1994) suggested that swimming at these depths may allow *transients* to detect prey visually, using the silhouettes of prey against downwelling surface light.

Prey detection. A variety of differences in the echolocation patterns of *residents* and *transients* have been reported (Barrett-Lennard et al. 1996a). Barrett-Lennard et al. (1996a) noted that echolocation click trains produced by *transients* are of shorter duration than those produced by *residents*, and that *transient* click trains have unevenly spaced clicks while *resident* click trains are made up of evenly spaced clicks. *Transients* were also reported to use isolated clicks more frequently and to produce click trains less frequently than *residents*. Barrett-Lennard et al. (1996a) suggested that all of these differences arise from the differences in prey taken, since marine mammals can hear echolocation clicks and potentially evade capture while fish generally cannot. Several authors have suggested that killer whales do use passive listening to detect marine mammal prey (Barrett-Lennard et al. 1996a; Guinet 1992). Observations of marine mammals becoming silent and motionless in response to the presence or sounds of killer whales also support the use of passive listening in prey detection by killer whales (Jefferson et al. 1991). Even so, the relative roles of vision and passive listening in prey detection by *transients* remain unclear. Vision may be important in prey detection for several other species of marine carnivores; namely, sperm whales (*Physeter macrocephalus*) and white sharks (*Carcharhinus carcharias*) (Fristrup and Harbison 1993; Klimley 1994). Energy intake rates of *transients* hunting in areas with relatively high noise levels (namely, noises produced by a research vessel as well as other vessels in the area powered by outboard motors), which might mask the sounds of potential prey, were more than sufficient to meet the energetic needs of the whales (Baird and Dill 1996). Based on these observations and the diving pattern of the single *transient* studied, Baird (1994) suggested that vision may be regularly used to detect prey. *Residents* appear to locate prey underwater using a combination of echolocation and passive listening, and both vision and echolocation are probably important during prey capture (Barrett-Lennard et al. 1996a). *Residents* appear to spend much less time foraging at night than during the day; such a difference in activity state could reflect the importance of vision in prey

detection and capture (Baird et al. 1998). Killer whales occasionally use aerial vision to detect prey on beaches or on floating ice (Smith et al. 1981; Guinet 1992), where echolocation is ineffective.

Cooperative hunting and prey handling. Killer whales often forage in groups. Foraging in groups could occur due to an immediate benefit from group hunting or due to longer-term benefits of group living. Social functions of grouping in killer whales are discussed below. Immediate benefits of group hunting could involve an increase in the rate at which prey are encountered, an increase in prey capture success, a decrease in prey handling time (or reduced risks of prey capture), or an increase in the ability for groups to defend prey during intergroup conflicts.

In general, larger groups should have higher prey encounter rates (cf. Pitcher et al. 1982; Connor, chap. 8, this volume). If the prey (or the prey patch) is larger than can be consumed by a single individual, such an increase in encounter rates should favor larger group sizes. In theory, for prey that could be consumed by a single individual, larger groups would have to increase encounter rates beyond simply the additive effect of several individuals hunting together. One possible way in which encounter rates of marine mammal prey may increase in a multiplicative fashion is that potential prey may detect one whale in a foraging group and move away from its path of travel, effectively "blindly" entering the path of another forager while preoccupied with avoiding the first. Increases in prey encounter rates for larger groups have not been demonstrated with killer whales, but numerous authors have suggested that both *residents* and *transients* may benefit from cooperative food searching (Hoelzel and Osborne 1986; Ford 1989; Felleman et al. 1991; Hoelzel 1993; Baird and Dill 1996). Baird and Dill (1996) noted that for larger groups hunting pinnipeds, encounter rates could theoretically begin to decrease, as the likelihood that potential prey might detect the foraging group and escape onto shore or into underwater hiding sites should increase with predator group size.

In terms of an increase in prey capture rates with group size, more information is available, both for populations feeding on marine mammals and for those feeding on fish. Some mammalian prey, such as harbor seals, appear to "hide" at the bottom, perhaps in underwater caves or crevices (Baird and Dill 1995). In these cases, several individual *transients* appear to coordinate their surfacing patterns so that one whale is always at the bottom while the other replenishes its air, effectively waiting for the seal to run out of air (Baird and Dill 1995). Lone whales would have to

return to the surface to breathe, possibly allowing a seal to escape. For killer whales feeding on schooling herring off Norway, Similä and Ugarte (1993) describe whales circling under and around schools, apparently keeping the herring in a tight school and near the surface, where individual whales would strike the school with their tail flukes and eat individual fish. While no information was presented on whether larger groups of whales were more successful at corralling schools or at maintaining larger herring schools with fewer fish escaping, it appears unlikely that single or very small groups of whales could prevent the dispersal of herring schools.

Decreasing handling time or decreasing the risk of prey handling is likely to be important only for potentially dangerous prey, such as adult male sea lions or large whales. Killer whales appear to spend considerable time in the process of killing such prey, possibly to minimize the potential for injury (Baird and Dill 1995), and at least one case of a large sea lion escaping after having been caught has been reported (Bigg et al. 1987). For prey the size of harbor seals, no effect of group size on handling time was found; individual whales or whales in very small groups appear to be able to capture, kill, and eat harbor seals very quickly (e.g., in less than two minutes), although handling time is often extended for other, unknown reasons (Baird and Dill 1995).

Transients hunting primarily harbor seals had significantly higher food intake rates in groups of three than in groups of other sizes (either larger or smaller: Baird and Dill 1996) (fig. 5.5). The increase in foraging success with group size likely resulted from the synergistic effects of several individuals hunting together, by increasing both prey encounter and capture rates. For prey of a relatively constant size, as group size increases, competition over the carcass also increases; thus for larger prey, the optimal group size would likely be larger than three individuals (Baird and Dill 1996). Similarly, for dangerous (e.g., adult male Steller sea lions, *Eumetopias jubatus*) or more difficult to capture prey (e.g., Dall's porpoises, *Phocoenoides dalli*), an increase in group size should decrease costs of prey capture or increase prey capture rates (Baird and Dill 1996).

Large groups should be better able to defend prey patches or prey carcasses from smaller groups. Such intergroup conflicts over prey have not been observed for *resident* or *transient* killer whales in British Columbia, Washington, or Alaska but they have been reported elsewhere. Bisther and Vongraven (1995) observed occasional "feeding patch takeovers" off Norway, apparent competitive interactions in which one group of killer whales rapidly approached another that was feeding on a herring school,

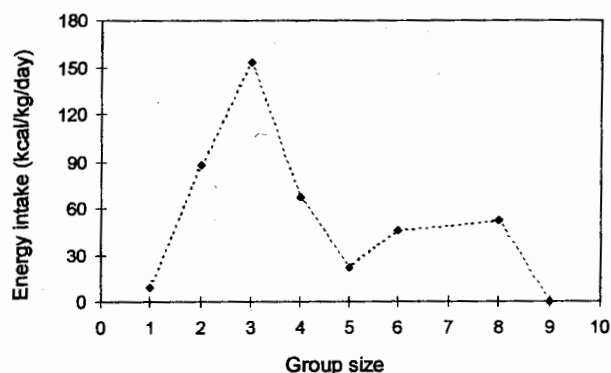


Figure 5.5. Energy intake (measured in kcal/kg/day) versus group size for *transient* killer whales, showing the clear peak in energy intake rates for individuals in groups of three. (From Baird and Dill 1996.)

with the original group leaving. No information was presented, however, on the relative size or usual association patterns of the respective groups. Hoelzel (1991a) noted similar behavior in killer whales feeding on sea lions off Argentina: a larger group of whales (seven individuals) appeared to actively displace a smaller group (two individuals) from the most productive foraging area. C. Guinet (personal communication) has also observed similar behavior on one occasion in the Crozet Archipelago, where a group of seven individuals appeared to take an elephant seal pup that had been killed by a group of five individuals.

Sharing of prey is occasionally observed among *residents* feeding on fish. Prey sharing, and even provisioning, is observed much more frequently among killer whales feeding on marine mammals (Hoelzel 1991a; Guinet 1992; Baird and Dill 1995). Baird and Dill (1995) suggested that prey sharing occurred in virtually all of the marine mammal attacks they observed. Hoelzel (1991a) observed prey sharing in all three groups he studied, and noted that one whale in each group did the majority of the hunting and provisioned the other whales in the group. Guinet (1992) observed prey sharing in twenty-seven of twenty-nine cases. One of the two cases in which sharing did not occur involved four consecutive elephant seal captures, in which the last seal in the series was consumed by only one of the whales present. The remaining case involved a single whale apparently searching to determine the location of the remainder of her group after capturing an elephant seal pup, then moving in the opposite direction to consume the prey alone (Guinet 1992).

Among *transients* in British Columbia, apparent cooperative foraging occasionally occurs between pods (that is, all members of two or occasionally three pods forage together and share prey captured). Multipod foraging associations

are likely to be most beneficial when *transients* are hunting prey that are difficult to capture or dangerous, yet they do occur when *transients* are hunting harbor seals, which are neither difficult to capture nor potentially dangerous (Baird and Dill 1996). Multipod foraging associations have not been observed among killer whales hunting pinnipeds off the Crozet Archipelago (Guinet 1992) or off Punta Norte (Hoelzel 1991a). When intentional stranding is the primary hunting tactic (as in these latter two localities), it is unlikely that additional individuals could increase the capture rate or decrease the risk. Off the Crozet Archipelago, where killer whale group size is typically small, larger groups of killer whales have been observed attacking large baleen whales (Guinet 1991b). Combined with such occurrences elsewhere (Silber et al. 1990; Jefferson et al. 1991), Guinet (1991b) suggested that temporary feeding associations do occur. For killer whales cooperatively feeding on herring off Norway, Similä and Ugarte (1993) noted that only one group would feed on a school of herring at a time.

Killer whale calves and young juveniles often are not involved in capturing prey that may be somewhat dangerous, such as during intentional strandings or attacks against large baleen whales (Guinet 1991a; Hoelzel 1991a). In general, though, killer whales of all ages and both sexes participate in marine mammal attacks and subsequent feeding (Jefferson et al. 1991). However, some sex-specific differences in hunting tactics have been noted for both mammal-eating and fish-eating killer whales. In British Columbia, male *resident* killer whales often forage in deeper water than do females, or in peripheral positions in a group. Since *residents* do not appear to cooperatively herd or chase prey, it has been suggested that such differences may be due to different diving capabilities of the sexes (which should correlate with size differences: Bain 1989). However, time-depth recorders deployed on both subadult and adult female *resident* killer whales in southern British Columbia did demonstrate their abilities to regularly use bottom areas in relatively deep (>150 m) waters (Baird 1994; Baird et al. 1998). J. K. Jacobsen (personal communication) observed *resident* killer whales occasionally attempting to capture fish (large salmon) that were trying to hide in rock crevices along the shoreline; only females and subadults were observed in this behavior. Due to the high degree of sexual dimorphism, adult males may be limited in their range of behaviors associated with prey capture in situations requiring extreme maneuverability or travel in shallow waters. Only females engage in intentional strandings to capture pinnipeds in the Crozet Archipelago (Guinet 1991a), while both males and females participate in intentional strandings to capture pinnipeds at Peninsula Valdés, Argentina

(Lopez and Lopez 1985). This difference may be due to the lower-grade slopes of the beaches in the Crozet Archipelago compared with Peninsula Valdéz: larger males may be unable to beach themselves successfully, or to do so without risk, at Crozet (Guinet 1991a, 1992). During attacks on a Bryde's whale (*Balaenoptera edeni*) and on Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), males have been noted to play a minimal role, if any, in the attack (Silber et al. 1990; Dahlheim and Towell 1994).

Among *transients* hunting harbor seals, males and females seem to play similar roles in finding and capturing seals, but occasionally differ in how they handle prey (Baird and Dill 1995). During several seal attacks, as a group of females and subadults would pass by a seal at the surface, striking it with their tails or pectoral flippers, an adult male in the group would appear to prolong its dive time, possibly staying beneath the seal to keep it from escaping (Baird and Dill 1995). Among killer whales searching for marine mammal prey along beaches in the Crozet Archipelago, in two different pods, individuals maintained specific foraging positions relative to other individuals, both within and between years and between different bays (Guinet 1992). Such differences, like the differences noted above with *transients* handling harbor seals, might be considered "division of labor" (cf. Stander 1992 for examples with lions), with specific individuals repeatedly taking the same role in hunting or prey handling. No apparent division of labor was observed for killer whales cooperatively feeding on schools of herring off Norway (Similä and Ugarte 1993).

Foraging tactics vary between populations, depending on habitat, type of prey taken, and factors such as prey abundance. Intentional stranding behavior to capture hauled-out pinnipeds is frequently observed in Argentina and the Crozet Archipelago. Such behavior is extremely rare for mammal-eating *transients* in British Columbia and Washington (Baird and Dill 1995). Two likely reasons exist for its rarity in those areas. One is that there appears to be a cost associated with the behavior. For example, in one case a juvenile killer whale intentionally stranded and was unable to return to the water on its own (it was pushed into the water by researchers) (Guinet 1991a). Six other stranded killer whales had been recorded on the Island over a twenty-seven-year period (five juveniles and one adult), implying that these individuals may have died as a result of intentional stranding (Guinet 1991a: he did not report, however, the sexes of the stranded individuals, whether any evidence was available that they had stranded intentionally, or whether all died). While mortality associated with intentional stranding may be extremely infrequent, the benefits would presumably have to be high to warrant this behavior.

The benefit in areas of high prey abundance, such as with harbor seals around southern Vancouver Island, is low, in that prey can be captured relatively easily without engaging in this behavior.

Killer whales off Norway use bubbles, lobtailing, and body pigmentation to herd and encircle herring, force them to the water's surface, and prevent them from escaping (Similä and Ugarte 1993). Whales were repeatedly observed swimming with their ventral surface toward the herring schools (which presents a white pattern bordered with black anteriorly, and a more complex black-and-white patterning posteriorly), often in response to movements of herring away from the school. Such behavior appeared to result in herring moving back into the school. The exact mechanism of such herding is unclear, as the white anterior area might function to tighten the herring school while the black-and-white posterior area of the ventral surface would be more likely to disrupt the herring schooling (Wilson et al. 1987).

Predation and Parasitism

No predators on killer whales have been recorded. Young or sick whales are likely potentially at risk from attacks by large sharks in some areas, but no observations of individuals with scars from failed shark attacks have been reported, as is seen with other dolphin species (e.g., Corkeron et al. 1987; Cockcroft et al. 1989; Connor et al., chap. 4, this volume). Scars from intraspecific interactions are frequently observed (Scheffer 1969; Visser 1998; fig. 5.6), but it is unknown whether such interactions ever result in mortality.

A variety of endoparasites have been recorded from killer whales, including trematodes, cestodes, and nematodes (reviewed in Heyning and Dahlheim 1988). Transmission of such parasites is primarily through ingestion of infected food items. External parasites are rarely seen, but some killer whales have been seen with barnacles on the rostrum, the trailing edge of the tail flukes, or the trailing edge of the dorsal fin, and with a species of cyamid ectoparasite. The probable cause of transmission of ectoparasites is body contact between individuals, both during social contacts and from mother to offspring.

Interspecific Associations

Killer whale interspecific associations are primarily thought to involve predation upon other species (fig. 5.7), although a variety of nonpredatory associations have also been observed. Unfortunately, many reports in the literature document interspecific associations but without the necessary behavioral detail to specify the form or type of association;

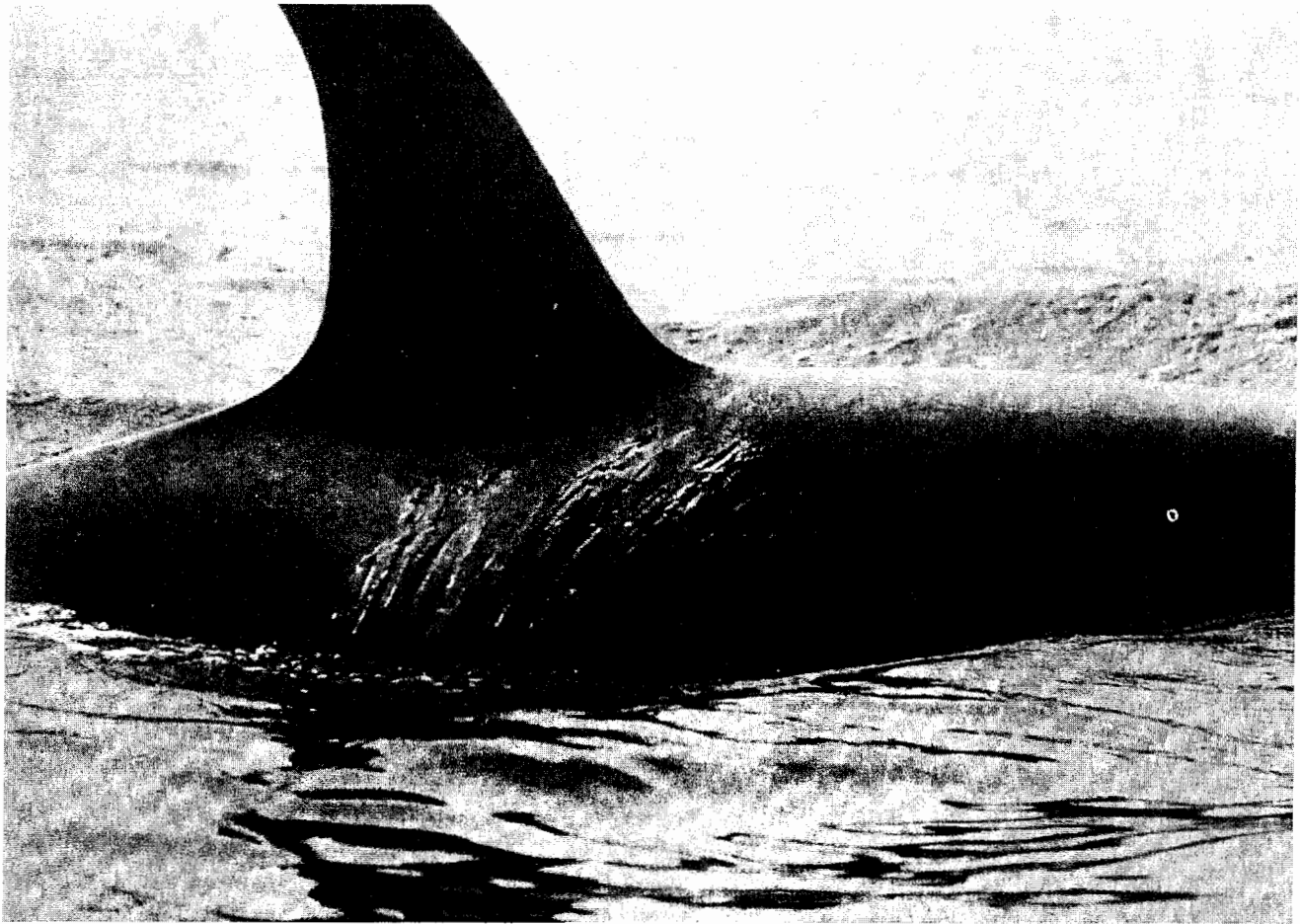


Figure 5.6. Fresh tooth rakes, most likely caused by another killer whale, on the side of a ten-year-old female "southern" *resident* off Victoria, British Columbia. (Photograph by Robin W. Baird.)

namely, predatory versus nonpredatory (e.g., Mikhalev et al. 1981). At least twenty-six species of cetaceans and seven species of pinnipeds have been observed associated with killer whales in nonpredatory contexts (Jefferson et al. 1991). Often such interspecific associations have involved the co-occurrence of killer whales and other species of marine mammals in the same area at the same time, with little or no behavioral interaction. Other times, however, both large and small cetaceans and pinnipeds have often apparently deliberately approached and interacted with killer whales. In some cases, such as those in British Columbia and Washington, these instances have involved *resident* killer whales, which are typically little threat to other marine mammals, but some have involved *transients*. Groups of sea lions occasionally jump into the water when *transients* are near and often follow the whales (R. W. Baird, personal observation). In large groups, the risk to an individual sea lion should be reduced due to dilution, and killer whales may be reluctant to attack a large group due to in-

creased risk of injury, thus the threat may be not be great in such situations. Harbor seals seem to be the preferred prey of *transients* in this area (Baird and Dill 1996), thus sea lions are at low risk of attack. Such behavior may function as a "pursuit invitation," alerting the whales that they have been detected and that the element of surprise is lost (Jefferson et al. 1991; Smythe 1970; Connor, chap. 8, this volume). It is also possible that sea lions benefit from such behavior by learning more about their predators; such information may be valuable at a later date if an individual is attacked, since such attacks are not always successful (Bigg et al. 1987).

Life History

Birth

The most detailed information on life history is for British Columbia *residents* (table 5.2); many of the characteristics

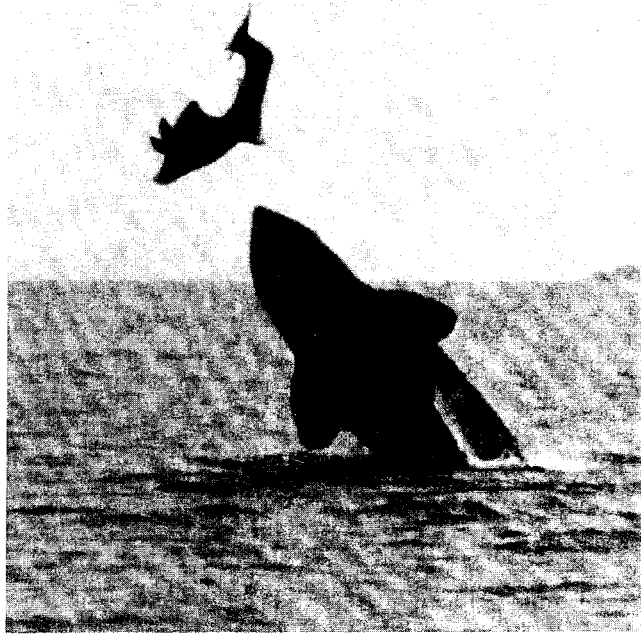


Figure 5.7. A *transient* killer whale throwing an adult male Dall's porpoise into the air, Chatham Strait, Alaska.
(Photograph by Robin W. Baird.)

likely vary between populations. Some information—for example, gestation period—has been best established with captive animals. Gestation periods in captive animals, measured using hormone levels, ranged from 468 to 539 days (average of 517 days; SD = 20 days) (Duffield et al. 1995). Length at birth in British Columbia and Washington ranges from at least 218 to 257 cm (Olesiuk et al. 1990). One animal was born in captivity at a length of 206 cm (Duffield and Miller 1988), while the largest fetus recorded worldwide appears to have been 270 cm in length (Nishiwaki and Handa 1958). A single calf is usually born, though Olesiuk et al. (1990) reported two cases of twins, one of which was subsequently determined to be a case of mismatching (J. K. B. Ford, personal communication). In the remaining case, both animals (a male and a female born in 1980) survived to at least thirteen years of age (Ford et al. 1994). If this situation is not a case of adoption (no adult females in that pod went missing that year: Olesiuk et al. 1990), then killer whales appear to be the only species of cetacean in which viable multiplerts have been recorded. Calving occurs year-round in British Columbia, but there appears to be a peak in births between fall and spring (Olesiuk et al. 1990). Definitions of the age at which individuals are no longer “calves” vary between studies.

Weaning and Interbirth Intervals

Precise age at weaning is not known, but killer whale infants begin taking solid food at a very young age. Heyning (1988) noted solid food and numerous parasitic nematodes (whose first hosts were fish) in the stomach of a 2.6 m long animal. No milk was visible in the stomach of that animal, but the contents were not tested for the presence of milk lactose. In other species (e.g., sperm whales), the presence of solid food in the stomach is known to be a poor method for estimating the age at weaning. Using the ages at which killer whales begin spending more time away from their mothers, as well as when they are observed taking fish, Haenel (1986) estimated weaning to occur at between one and a half and two years of age. Weaning in at least one other species of odontocete, the bottlenose dolphin (*Tursiops* spp.), does not occur until about three or four years of age, even though calves begin capturing their own fish by six months of age (Connor et al., chap. 4, this volume), so it is likely that nursing in killer whales may continue beyond the ages suggested by Heyning (1988) or Haenel (1986). Guinet and Bouvier (1995) noted that killer whales appear to first be able to successfully capture elephant seal pups by intentional stranding at about six years of age, and thus suggested that they are still somewhat dependent on adults at that age.

Olesiuk et al. (1990) noted that calving interval, defined as the interval between births of surviving calves, ranges from two to twelve years in British Columbia (mean = 5).

Table 5.2. Life history characteristics of killer whales

Maximum body size: female	7.7 m
Maximum body size: male	9.0 m
Gestation length ^a	Mean = 517 days; range = 468–539 days
Weaning age	??
Interbirth interval ^b	Mean = 5 years; range = 2–14 years
Calf mortality (to 6 months) ^b	37–50%
Length of estrous cycle ^a	Mean = 42 days; range = 23–49 days
Calving season ^b	Year-round with winter peak
Age of female sexual maturity (first birth) ^b	Mean = 15 years; range = 11–20 years
Age of male sexual maturity (asymptotic growth) ^b	20 years
Maximum life span: female ^b	80–90 years
Maximum life span: male ^b	50–60 years

^aData from Robeck et al. 1993.

^bValues derived from studies of *resident* killer whales from British Columbia and Washington (Ford et al. 1994; Olesiuk et al. 1990).

Subsequent to their study, one fourteen-year calving interval was noted in the same population (Ford et al. 1994). The occurrence of two-year calving intervals implies that females are able to become pregnant while still nursing a calf. In Prince William Sound, calving interval has been observed to range between four and ten years (Matkin and Saulitis 1994). Calving interval increases slightly with age, but there is extremely high variability (Olesiuk et al. 1990).

Mortality and Life Expectancy

Mortality rates for British Columbia and Washington *residents* vary with age and, for older individuals, with sex (Olesiuk et al. 1990). Neonatal mortality, defined as that which occurs between birth and six months of age, is very high. Olesiuk et al. (1990) estimated neonatal mortality of *residents* in two ways, using survival rates of calves first encountered during winter and using the discovery of stranded animals. These estimates were 37% and 50%, respectively. Bain (1990) independently estimated neonatal mortality in the population of *resident* killer whales off northern Vancouver Island at 42%, based on the distribution of calving intervals. The causes of this high neonatal mortality remain unclear, but similar neonatal mortality levels have been noted for bottlenose dolphins (Connor et al., chap. 4, this volume). Predation does not appear to be a significant cause of mortality in the *resident* populations; no individuals appear to have scars associated with failed shark attacks, and stranded animals that have been found show no evidence of predatory attacks. Unfortunately, detailed postmortem examinations of stranded neonates from these populations have been undertaken on only one individual, and the cause of death was not determined (R. W. Baird, unpublished data).

After six months of age, mortality rates decline steadily for both sexes. Mortality rates are lowest around twelve to thirteen years of age for males, and around twenty years of age for females, after which mortality rates begin to increase steadily with age (Olesiuk et al. 1990). Maximum longevity has been estimated at about fifty to sixty years for males and eighty to ninety years for females. At birth, average life expectancy is about twenty-nine years and seventeen years for females and males respectively. From six months of age (excluding the high mortality rate during the first six months), average life expectancy increases to about fifty years for females and about twenty-nine years for males. Life expectancy at sexual maturity (assumed to occur at about fifteen years of age for both males and females: see discussion below) is about sixty-three years for females and thirty-six years for males (Olesiuk et al. 1990). The causes

of the shorter life expectancy of males are unknown, but are presumably somehow related to sexual selection.

Growth and Age at Sexual Maturity

Based on captive data, growth rates are similar for males and females. Growth rates tend to be linear for the first nine to twelve years for females and for the first twelve to sixteen years for males, after which both sexes show a decrease in growth rate (fig. 5.8; Bigg 1982; Duffield and Miller 1988). However, growth rates vary between individuals as well as between and potentially within populations (Duffield and Miller 1988). The mean annual growth rate for six eastern North Pacific killer whales was 38 cm per year (range 26–53 cm/yr). Growth rates of North Atlantic killer whales fell into two distinct categories, those that grew at about 21 cm per year (range 17–25 cm/yr) and those that grew at about 39 cm per year (range 31–48 cm/yr) (Duffield and Miller 1988). Based on whaling data, Christensen (1984) suggested that growth rates of wild killer whales off Norway are not linear with age, and that males may show a secondary growth spurt associated with adolescence. However, lengths reported were estimates rather than precise measurements; thus, the validity of these conclusions is unclear. The maximum lengths recorded for males and females are 9.0 m and 7.7 m respectively (Heyning and Brownell 1990), although average maximum sizes attained by both sexes appear to be much smaller (Duffield and Miller 1988).

Age at sexual maturity for females has been reported in a variety of ways, including age at first ovulation, age at first pregnancy, and age at first parturition. Olesiuk et al. (1990) defined age at sexual maturity for females as the age at which they first give birth to a viable calf, and noted

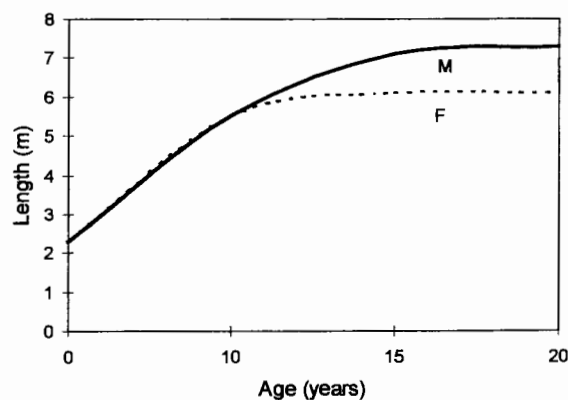


Figure 5.8. Theoretical average growth curves for eastern North Pacific killer whales based on measurements from captive animals. (After Duffield and Miller 1988.)

that it varies between twelve and sixteen years (mean = 14.9). Since their study, one female in the same population has given birth at eleven years of age (Ford et al. 1994). Ford et al. (1994) show one female giving birth at ten years of age, however, the age of that female was estimated plus or minus one year (Olesiuk et al. 1990). Similarly, the upper limit for the age at which females give birth to their first viable offspring has risen, with two females first giving birth at twenty years of age (Ford et al. 1994). Age at first parturition (for viable calves) in captive animals has averaged 12.7 years (range 8–15; Duffield et al. 1995). It is unclear, however, whether such pregnancies of younger animals would be unsuccessful in wild individuals, or just do not occur, being suppressed either behaviorally or physiologically. Olesiuk et al. (1990) also noted that fecundity rate (defined as the proportion of mature females that give birth to viable calves each year) declines linearly with age. However, this conclusion is sensitive to age estimation techniques for older females. Some females in their study that were adult-sized at the beginning of the study period (in the early 1970s) and were not recorded to have given birth during the study were assumed to be older individuals. Females appear to become reproductively senescent at a mean age of about forty years (though one female reproduced at approximately fifty years of age) (Olesiuk et al. 1990). This supposition is based on several findings. About seventeen females that were adult-sized at the beginning of the study, and which were still alive as of 1993, have never been observed with calves (Ford et al. 1994). An additional seven adult females died ten or more years after first being encountered without ever having been recorded with a calf (Ford et al. 1994). However, a very small proportion of individuals may be infertile, due perhaps to disease or congenital problems. Evidence for this conclusion comes from one southern *resident* individual of known age (\pm two or three years), who matured in the mid- to late seventies but has not been known to have given birth to a calf as of mid-1999, despite being observed regularly each summer every year since she matured. Regardless, the relatively small proportion of such infertile females among those born into the population in the last thirty years makes it likely that some females do live twenty or more years after reproductive senescence (that is, are postreproductive).

Appendage size differs between the sexes, with adult males having larger pectoral fins and tail flukes than adult females. Adult males have a tall, triangular dorsal fin that may reach up to 1.8 m in height, while in juvenile males and adult females the fin reaches 0.9 m or less and is generally more falcate (fig. 5.9). Onset of sexual maturity for

males has been defined by an increase in the growth rate of the dorsal fin (Olesiuk et al. 1990). Using this criterion, onset of sexual maturity for males ranges from ten to seventeen and a half years (mean = 15) (Olesiuk et al. 1990). The use of such a criterion, however, needs to be tested using hormonal levels, perhaps with captive animals. Dorsal fin growth for males continues for at least six years after the onset of maturity, and physical maturity may be reached at the end of that period (Olesiuk et al. 1990).

Social Behavior and Communication

Preferential associations both within and between groups have been reported at different field sites; these include female-calf, male-calf, all-male, and multigroup associations. Seasonal changes in behavior have been noted for *transients* in British Columbia and for killer whales in the Crozet Archipelago. In both cases, an increase in social behavior has been demonstrated during the period when prey abundance is highest (Baird and Dill 1995; Guinet 1991b).

Interactions with Young

Observations of killer whale births in the wild have been documented on two occasions, and both involved the mother giving birth among a larger group of related individuals (e.g., Stacey and Baird 1997). In both cases, considerable percussive activity by other individuals present and rubbing and lifting the infant into the air was observed (Stacey and Baird 1997). The relationship between a mother and her calf is not abruptly interrupted as the latter matures (Haenel 1986). Calves do tend to spend less time with their mothers as they grow, because they start swimming with other members of the pod. Among *residents*, even though a juvenile decreases its dependence on its mother, they will never be completely separated for long periods. Associations between infants and individuals other than the mother fall into several categories. Multi-calf play groups occasionally form. Older individuals, including subadults and both adult females and males, associate with infants. Such behavior has often been referred to as alloparental or allomaternal care (Haenel 1986; Bain 1989; Rose 1992; Bisther and Vongraven 1995). It is unclear, however, whether and how such behavior benefits the calf or its mother. Data on young calves (those under one year of age) associating with individuals other than their mothers are rare, and the necessary detailed behavioral data (e.g., activity, travel speed, respiration rate) on mothers with and without calves, and on calves with their mothers, alone, and with other individuals, are lacking.

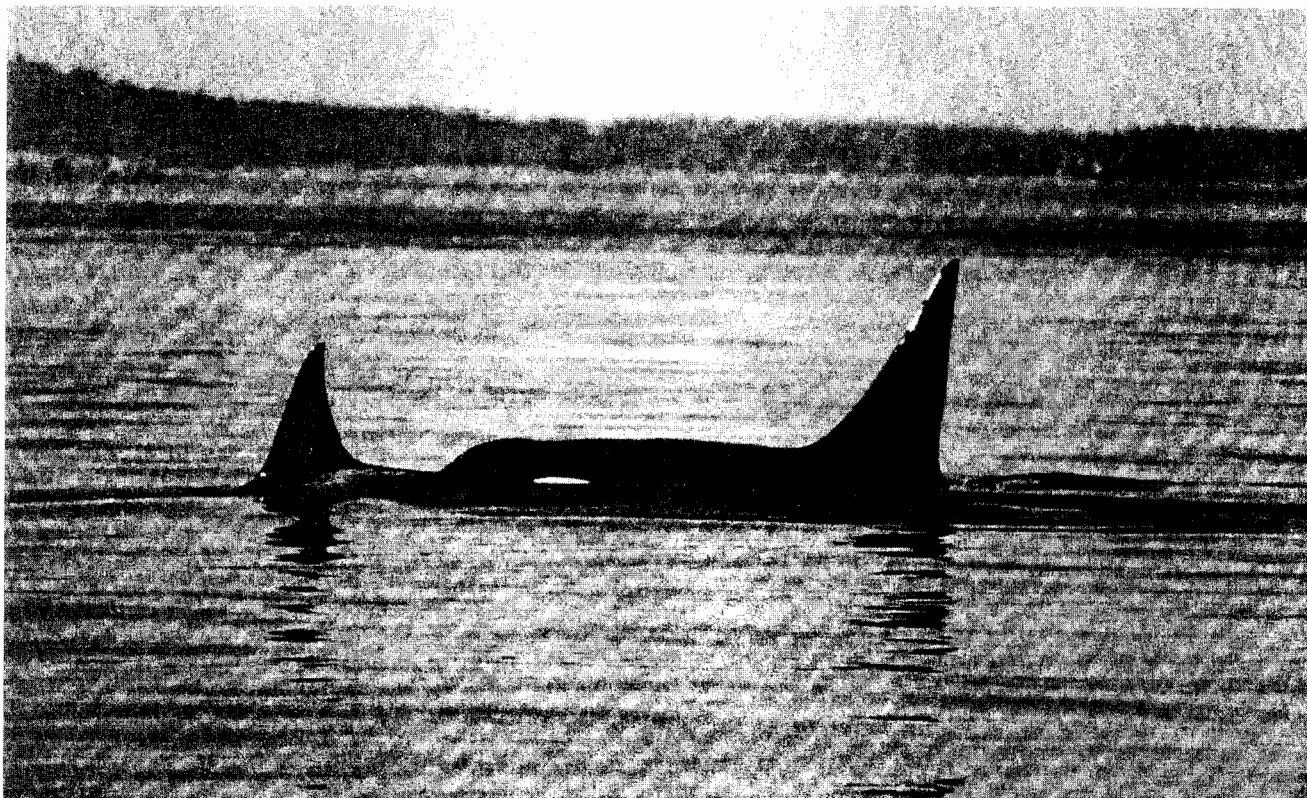


Figure 5.9. Adult female (*left*) and adult male (*right*) transient killer whales, showing the smaller and more falcate dorsal fin of the female. Adult males also have larger pectoral flippers and tail flukes than females. (Photograph by Robin W. Baird.)

Adults may teach young to hunt, based on observations of coordinated intentional strandings between an adult and a juvenile, in which the adult would capture a prey item and pass it to the juvenile (Lopez and Lopez 1985). In their review of teaching in nonhuman animals, Caro and Hauser (1992) noted that the evidence for teaching by killer whales was weak. They defined teaching as a modification of behavior only in the presence of a naive observer, which involves a demonstrated cost for the teacher (or lack of immediate benefit) and a demonstrated benefit for the observer that would not have occurred in the absence of teaching. Information collected subsequent to Lopez and Lopez's study provides further evidence for teaching by killer whales. Several types of costs associated with purported teaching events have been identified. One individual adult female had decreased capture success when hunting in close proximity to two juveniles (Hoelzel 1991a). As mentioned previously, Guinet (1991a) noted a risk of mortality associated with intentional strandings, apparently greatest for juveniles, though some risk may occur for adults as well. Evidence on benefits to young would need to compare success rates of calves that beach with potential adult "teachers"

versus those that beach alone, as well as those that beach frequently versus rarely. That some individuals are better hunters than others, and that even adults practice hunting techniques, has been demonstrated (Hoelzel 1991a; Guinet 1991a). Guinet (1991a) also provided additional information relevant to the issue of whether teaching occurs. Intentional strandings in the Crozet Archipelago appear to be of two types, those directly intended to capture prey, and coordinated group strandings (when no prey are on the beach), which appear to be a form of social play (Guinet 1991a). Only a few females (all adults) engaged in strandings to capture prey, while all juveniles and the other adult females engaged in coordinated group strandings (Guinet 1991a). Guinet (1991a) also noted association patterns between stranding individuals. Unlike the situation in Patagonia, group strandings did not involve the capture of prey or appear to represent failed attacks, thus adults received no energetic benefit of the behavior. The most unusual pattern was that one juvenile associated more frequently with an adult female that regularly hunted by intentional stranding than it did with its mother (who had not been recorded capturing prey by intentional stranding). It appears that

the juvenile preferentially associated with the adult from whom it could benefit the most, in terms of learning successful hunting techniques, rather than with its mother, with whom it associated in all other contexts (traveling, resting, feeding). One of the primary problems with the killer whale data in terms of Caro and Hauser's (1992) definition of teaching is that the adult whales also exhibit the behavior (intentional stranding not associated with prey capture) in the absence of potential pupils (although they could have been doing so to practice the hunting technique themselves). Guinet (1991a) noted some modification of adult behaviors when calves or juveniles participated, however, in that adults returned to the water at the side of the calves, helping them roll back into the water. One instance of a female pushing her infant onto shore to strand it, then stranding beside it to assist it back into the water, also suggests that teaching is occurring.

Male Behavior and Relationships

For northern *resident* killer whales, a variety of individual and age-specific relationships between males and other age-sex classes have been described (Rose 1992). Subadult and juvenile males occasionally aggregate in "play" groups, in which frequent body contact, splashing, and sexual behavior is observed. The latter consists of penile erections and/or beak-genital orientation by one or both males. These activities may be performed by more than two males and with males of different age classes. To test whether these male-only social groups represented agonistic/dominance interactions or play, Rose (1992) examined age distribution, relatedness of participants, and reciprocity of physical contact, among other parameters. These groups most frequently involved animals of different age classes, and specific behaviors exhibited were usually reciprocated. Trios and quartets frequently occurred (one-third of all male-only groups observed), and individuals did not appear to actively try to avoid larger (thus potentially dominant) whales. As such, Rose (1992) suggested that these associations were more likely to represent play groups than agonistic interactions. Adolescents participated in such interactions four times as often as adults, and Rose (1992) suggested that these associations may help adolescents gain courtship skills. In comparing her observations of male social behavior with the results of other killer whale studies, Rose (1992) stated that males, and particularly young males (from twelve to twenty-five years), socialize more, and more vigorously, than females. However, methodological differences between studies suggest that this question warrants further attention, particularly quantification of female social behavior using focal animal sampling. Sex dif-

ferences in patterns of play have been observed in some primates (with juvenile males of some species playing more than juvenile females) and may be related to development of fighting skills (Fagen 1993).

Vocalizations

Killer whale vocalizations have been grouped into three distinct categories: whistles, discrete calls, and clicks (Ford 1989). Research efforts have focused on the latter two types of vocalizations. Studies of the communicative functions of such vocalizations have been hampered by the difficulty of localizing underwater sounds and of recording high-frequency sounds, both of which require specialized equipment (see Miller and Tyack 1998). No published studies using sounds localized from specific individuals are available, but some higher-frequency work has been undertaken on echolocation clicks. Ford (1989) suggested that discrete calls produced by *resident* killer whales function as social signals between pod members, because production of calls seems to elicit calls from other individuals, and call and whistle rates are highest when whales are socializing. As for the communicative function of echolocation clicks, Barrett-Lennard et al. (1996a) noted that while production of click trains from one individual did not elicit click responses from other individuals, click trains were frequently produced during social interactions of *residents*. However, no detailed analysis of killer whale echolocation clicks and their potential communicative function has been undertaken (cf. Dawson 1991 for a study of Hector's dolphin, *Cephalorhynchus hectori*, clicks and communication). Based on a negative correlation between group size and echolocation use for *residents*, Barrett-Lennard et al. (1996a) suggested that information collected through echolocation is shared between individuals. However, their study did not appear to control for group size effects on behavior, which have been documented for both *residents* and *transients*. In a study of southern *residents*, group size and the occurrence of fast, nondirectional surfacings (which were interpreted as indicative of feeding) were negatively correlated (Hoelzel 1993). For *transients*, social behavior increased with group size, while foraging behavior decreased with group size (Baird and Dill 1995). Since feeding seems to occur less frequently in larger groups of both *residents* and *transients*, a decrease in echolocation would be expected for that reason alone. Thus it is unclear whether such sharing of information actually occurs.

Killer whales exhibit a variety of percussive behaviors, such as breaching (fig. 5.10), tail slaps, pectoral fin slaps, and dorsal fin slaps. Norris and Dohl (1980b) have suggested that such behavior may function as a means of com-



Figure 5.10. An adult male *transient* breaching, a behavior that usually occurs only after a prey capture or when multipod groups are engaged in social behavior. Such behaviors are probably infrequent at other times for *transients* due to their potential negative effects on foraging success, since marine mammal prey such as harbor seals could easily detect them. (Photograph by Robin W. Baird.)

munication between individuals, though this has not been rigorously tested with killer whales. The role of body posturing or touching between individuals has not been investigated as to potential communicative functions.

Socioecology

Resident killer whales are members of the only mammalian population in which no dispersal of either sex has been recorded. Male-biased dispersal and female philopatry is the most common pattern observed in mammalian populations (Greenwood 1980; Clutton-Brock 1989). When male killer whales stay within their natal group, it is likely because the costs of staying are low and/or because there are some benefits to staying. Direct costs of staying in the maternal group could include decreased opportunities for mating or energetic costs associated with increased competition for food. However, because of their wide-ranging movements and regular interactions between pods, oppor-

tunities for mating may not be lower for killer whales that remain within their maternal group (Baird 1995; Connor, chap. 8, this volume). Bain (1989) suggests that potential costs of competition for food for *residents* are reduced, as adult males should be able to feed at greater depths and on larger prey items, essentially dispersing ecologically, not geographically (although the time-depth recorder work of Baird et al. [1998] suggests that females and subadults can dive as deeply as adult males, at least in the inshore waters around southern Vancouver Island). Potential benefits of staying, in terms of inclusive fitness, could include assisting with the care of related calves within the group, assisting with group defense (as in *transients* defending against potential attacks by *residents*, or vice versa, or through competition between *resident* communities), or helping the pod to locate and capture prey. For *residents* in British Columbia and Washington eating fish, cooperating to capture prey may not be important, but among fish-eating whales elsewhere, such as off Norway, all individuals appear to

cooperate in herding fish. Increased access to mates is an additional potential benefit of philopatry for males, as brothers might form coalitions (Bain 1989), or mothers might help their adult sons gain access to mates (Connor et al., chap. 10, this volume). The costs for a female *resident* of remaining philopatric are also likely to be low for the same reasons: mating likely occurs between pods and not within, so selection for dispersal to avoid inbreeding is probably low. Females may benefit for other similar reasons as well: the increase in inclusive fitness associated with the care of related calves within the group, group defense, and locating prey schools.

There is an extremely wide range in pod sizes for *resident* killer whales (from three to fifty-nine individuals). Some of this variability is likely due to chance demographic circumstances. Small pods in which the surviving offspring of a lone adult female are all males are destined to die off, and in fact, several northern *resident* pods or subpods appear to be doing exactly that (Ford et al. 1994). This wide variability, as well as the observation that these smaller pods or subpods do not join with other groups, suggests that selection pressure on group size for *residents* is not strong. This supposition is supported by the analysis of Brault and Caswell (1993), who found no significant demographic effects of pod size. This variability contrasts strikingly with the small variability observed for *transient* pod sizes (Baird and Dill 1996), from one to four individuals. Selective pressure favoring small pods, due to the energetic costs of foraging in large groups when hunting marine mammals, appears much stronger in this circumstance. Alternatively, a small pod joining with a larger pod for a long period might not be an option if the larger group actively worked to prevent such joining (although cf. Giraldeau and Caraco 1993).

For *transients*, remaining in a group larger than three has a direct cost in terms of a reduced energy intake rate (Baird and Dill 1996). When adult and subadult individuals are foraging, they are found most frequently in groups of three, the group size at which individual energy intake rates are maximized (Baird and Dill 1996; see fig. 5.5). Dispersal of both sexes from groups larger than three or four individuals likely occurs in response to the energetic costs associated with remaining in a large maternal group. Groups larger than three or four individuals are regularly observed nonetheless (the largest documented in Baird and Dill's study was fifteen individuals), and the benefits of the occasional formation of such large groups may outweigh the short-term energetic costs. Social behavior is more common than foraging in larger groups of *transients*, and these

large groups may provide opportunities for mating, allo-maternal care, and/or learning mating or courtship skills (Baird and Dill 1995). Larger groups of *transients* also contain a disproportionately large number of calves and juveniles, and these groups may function to protect these more vulnerable individuals from attacks by *residents* (Baird and Dill 1996).

While the data are incomplete, a picture of the social system and social organization of *transients* can be suggested (fig. 5.11). The choice of social partners for a female *transient* varies according to a variety of factors, including her age, the number and age of her siblings, and the number, age, and sex of her offspring. Juvenile females appear to remain with their mothers until they reach reproductive age. At that time, two possibilities seem apparent. One is that her maternal pod will accept the presence of an adult male for a period of time, despite the energetic costs of an additional individual in the group, to allow mating to occur. How such males are chosen is unclear. The other possibility is that she will begin to travel for periods of time with one or more *transient* pods that contain an adult male. Despite the energetic costs to the individuals in the pod containing the adult male, such pods are probably willing to accept a reproductive female for the sake of his opportunity to mate. This latter scenario is more likely to occur when the female's maternal group has already reached a size of four individuals; thus, in terms of inclusive fitness, an energetic benefit exists to leaving (cf. Giraldeau and Caraco 1993). If a female who has dispersed loses her calf or is unable to conceive, she may return to her natal pod, assuming that returning does not increase its size above the optimum. Once a female gives birth, or if she has two juvenile or infant offspring, she appears to spend several years temporarily associating with one or more pods of *transients*. I suggest that these temporary associations function to protect the offspring of the female from attacks by *residents*. As noted, although one attack by *residents* on a *transient* pod has been recorded, it is unclear why *residents* would attack *transients* (though one possibility is that *transient* pods occasionally pose a threat to *residents*, particularly to small groups or sick individuals). Attacks on adults by other *transients* are unlikely. Unless a clear numerical advantage is available for an attacking group, the risk of injury associated with such an attack would probably be too high. As well, *transients* benefit from the occasional temporary foraging associations needed to subdue difficult-to-capture prey, and aggression between *transient* groups could disrupt their future ability to cooperate.

The presence of a female and her offspring brings an

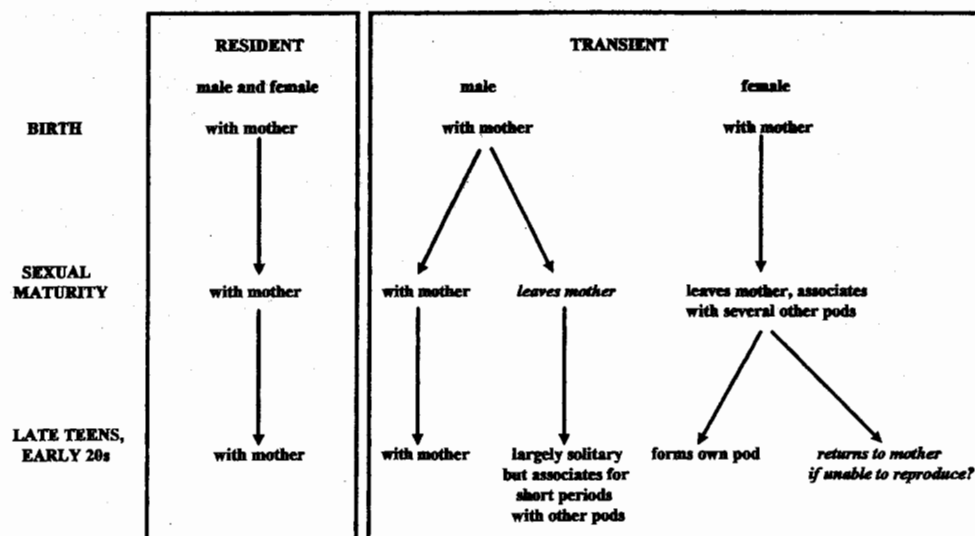


Figure 5.11. A diagrammatic representation of *resident/transient* differences in the patterns of association between mother and offspring, from birth through the early twenties. Those links labeled in italics are the most speculative, since the absolute occurrence of events to support such outcomes is rare, given the small population size, long periods between resightings of individuals, and long life span of these animals.

energetic cost to the members of the group she joins. Again, such pods may be willing to accept the female and her calf if the female gives adult males within the pod opportunities for mating. If there is a nonzero probability of a male fathering the female's next calf, or of being the father of her existing calf, other individuals in the group may also gain inclusive fitness benefits. Thus the increased probability of reproductive success for males within the group outweighs the short-term energetic costs. As her offspring age, and at least one (either a male or female) becomes old enough to assist the mother with group defense and foraging, she will then spend the majority of her time traveling only with those individuals.

Males appear to have two options for dispersal, depending on their relative position within their maternal group. A first-born male may stay with his mother his entire life, while other males disperse from their maternal group (while remaining within their natal range) sometime before sexual maturity is reached. For males, remaining philopatric is likely to be the preferred strategy. The first-born male, because of his larger size, is probably able to retain his position within the maternal group, from which he benefits in two ways: by increased energy intake rates associated with hunting in a group of two or three individuals, and by associating with his mother as an alliance partner (Connor et al., chap. 10, this volume) or in defense against *residents*. With the long interbirth interval, it is un-

likely that a second-born male will reach sufficient size and strength to be able to challenge an older brother for many years. Dispersing males appear to remain solitary for a large proportion of their time and thus suffer a direct energetic cost of dispersing (Baird and Dill 1996). Such males do associate for temporary periods with other pods, both those that already contain an adult male and those that do not. Although the data are limited, associations with pods that already contain an adult male appear to be of shorter duration than those with pods in which adult males are absent (R. W. Baird, unpublished data). Males are likely to be accepted into groups for longer periods when the group contains one or more young whales but lacks an adult male, as their presence may be valuable to the group in terms of defense against attacks by *residents*. Lone *transient* males do not appear to join with other lone males. One interaction observed between two lone males passing within 500 m of each other involved considerable percussive behavior by one individual, but both whales continued their routes of travel past each other (R. W. Baird, personal observation). It is surprising that lone males do not associate in pairs, considering the extensive energetic benefits associated with foraging in groups of two or three versus foraging alone (Baird and Dill 1996). Pair formation could theoretically confer benefits in terms of increasing mating success, if a pair of males were more able to mate with a female, or to prevent the female from mating with other males. The lack

of such pair formation, especially considering its foraging advantages, suggests that any increase in the ability to sequester females by pair formation would be outweighed by the reduced likelihood of paternity (see Connor et al., chap. 10, this volume).

The Future of the Taxon: Conservation Status and Critical Research Issues

In general, most killer whale populations have probably been affected by human activities to a relatively small degree when compared with other marine mammal species. Killer whales have been hunted for oil and meat (for human or animal consumption, fertilizer, or bait) in many areas, but particularly the western North Pacific (off Japan), the eastern North Atlantic, and the Antarctic (Berzin and Vladimirov 1983; Bloch and Lockyer 1988; Oien 1988; Reeves and Mitchell 1988b; Hoyt 1990). These fisheries have been discontinued since the early 1980s, and only very small numbers are taken occasionally today, either directly or incidentally (IWC 1993). Culling of animals, because of their perceived or known threat to fisheries, has also occurred (Dahlheim 1988; Olesiuk et al. 1990). Live-capture fisheries for public display in oceanaria have been focused in three areas, British Columbia and Washington, Iceland, and Japan (Hoyt 1992). While only small numbers of animals were taken, these takes had a substantial effect on local population sizes in British Columbia and Washington (Olesiuk et al. 1990). While the population of *resident* killer whales off northern Vancouver Island has recovered to levels higher than those prior to the live-capture operations (Olesiuk et al. 1990), southern *resident* killer whale population growth has been more sporadic, and the population has recently been declining (Baird 1999). Considering the extensive whaling takes off Japan from the early 1950s through the early 1980s (summarized in Hoyt 1990), even the small number of animals (five) live-captured off Japan in 1997 could jeopardize the recovery of the local population.

In recent years, nonconsumptive utilization of killer whales—that is, whale-watching—has become particularly prominent in Washington and British Columbia. These activities have raised a variety of concerns among researchers and members of the public as to the potential for disturbance in what are generally considered important feeding areas (Kruse 1991; Duffus and Dearden 1992, 1993; Phillips and Baird 1993; Duffus and Baird 1995). The available evidence for effects of boats on whale behavior or occurrence is generally unclear, and research on these interactions is continuing.

Killer whales have been shown to have among the highest levels of contaminants of any cetacean worldwide (Calambokidis et al. 1990). Surprisingly, levels of mercury appear to be higher in the tissues of *resident* whales than in *transients*, an unexpected trend considering the relative trophic levels of the two forms. Presumably such levels reflect consumption of heavily contaminated prey, but such prey consumption has not become apparent in the observational studies of foraging undertaken to date. The deployment of TDRs has suggested more extensive foraging on bottom or midwater fish than previously expected, thus identifying a possible source for higher levels of heavy metals (Baird 1994). TDR deployments on larger numbers of individuals in a wider variety of circumstances, behaviorally, temporally, and geographically, may also help better elucidate the regions of the water column where *residents* forage. Further work on year-round habitat use, perhaps through the deployment of satellite tags, is also necessary to identify general movement patterns during the winter months. These two areas of investigation are necessary if a potential source of contaminants is to be identified (and would also be of great value in understanding other aspects of killer whale biology). Little is known about the potential effects of such contaminants, and further research is also needed on that subject. Toxins such as spilled oils probably have an acute effect (Dahlheim and Matkin 1994).

The potential for direct competition with humans for marine resources, or for indirect interactions through the food web, has been virtually unexplored (Baird et al. 1992). The major prey populations of both *residents* and *transients* in the nearshore waters of the eastern North Pacific (salmon and seals) have been substantially reduced in size in the last hundred years, yet nothing is known about the potential effects of these reductions on top-level predators.

One of the most interesting aspects of killer whales is their extreme variability in foraging tactics, behavior, and dispersal patterns, even within one geographic area. Perhaps the most interesting questions that can be addressed for killer whales concern some of the causes and consequences of this variability. Better documentation of killer whale populations in areas outside British Columbia and Washington, to show whether such variability occurs elsewhere and what variations exist depending on the particular ecological circumstances in each area, is needed to address these questions. In terms of better understanding the relationship between *resident* and *transient* killer whales, several areas of research should be pursued. One is the determination of a behavioral isolating mechanism, and the clear differences in underwater sounds produced by the two forms is the obvious candidate. The role that pod- or

community-specific dialects may play in isolating these groups socially could be investigated by monitoring the reactions of *transients* to playbacks of *resident* sounds, and vice versa, as well as playbacks of the calls of northern and southern *residents* to each other. The diversity of playback circumstances would provide a clear experimental forum for understanding how *transients* and *residents* might interact upon meeting, a situation that is rarely observed in the wild, yet may have important implications for population structure. The possible differences in body size of offshore killer whales from either *residents* or *transients* could be investigated using photogrammetry (as could potential morphological differences between *residents* and *transients*). Another approach is examining the consequences of reproductive isolation between the two forms in terms of any skeletal or other morphological differences that may exist.

Further investigation of genetic differences at all levels of social organization is needed. This approach could include more detailed studies of population-level differences between offshore, *resident*, and *transient* populations, between northern and southern *residents*, and between those whales and populations of *resident*-type whales identified in the contiguous area farther north in Alaska and off California and Mexico, as well as within-group genetic variability. Genetic analysis of paternity could be used to interpret social behavior and to determine male and female mating strategies. For *transients*, analyses of relatedness for groups not regularly observed together could be used to confirm more cases of dispersal and provide more concrete evidence for the rules of dispersal that *transients* follow. Genetic data could also be used to examine relatedness between individual *transients* that share similar foraging specializations (nearshore versus offshore foragers). In theory, *transients* from different pods that share similar foraging tactics should be more strongly related maternally than paternally, assuming that such foraging tactics are learned and passed on maternally.

While research on killer whales worldwide has been concentrated in the research sites I focus on here, efforts are

being made to initiate studies of killer whales elsewhere. Further support for studies examining populations at the fringes of the well-established research sites, as well as more isolated populations, will greatly increase our knowledge of home range size and population variability respectively. At all sites, research on nighttime behavior has been virtually nonexistent, as has been work on offshore movements or populations. Research in virtually all areas has also had a strong seasonal bias, with research being undertaken when prey abundance is highest. Detailed studies of behavior, social organization, and ecology are needed during other seasons, when prey is likely to be more limiting. These studies could be combined with acoustic measurements of blubber thickness of known, free-ranging animals (M. Moore, personal communication) to examine how reduced prey availability, and thus presumably reduced energy stores, affect social behavior, as well as to correlate reproductive success with energy stores.

Even though many detailed behavioral studies have been undertaken, their reliance on methods of observing groups, rather than individuals, has limited the conclusions of many studies and has made comparisons with studies of other animals difficult, if not impossible (Mann, chap. 2, this volume). Further focal animal studies will be valuable. These could include studies of the relationship between infants and their mothers and other individuals in terms of the potential costs and benefits of allomaternal behavior, and of the relationship between postreproductive females and other individuals in the population, in terms of selective pressures favoring survival beyond reproductive senescence for females. The differing methods of researchers working on different populations of killer whales have also made comparisons difficult, and multipopulation behavioral research studies would be of value. Combined with the continuation of the long-term studies discussed here, such work will lead to a much greater understanding of the complexities of behavior and social organization of killer whales.

CETACEAN SOCIETIES

Field Studies of

Dolphins and Whales

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